Supplementary Information

SI 1. Archaeological Context

A summary of the archaeological information for all samples can be found in Supplementary Table 1. All calibrated dates are taken from CALIB 7.1 after Reimer *et al.* 2013[1] and reported at two standard deviations (95.4% confidence). The median probabilities (cal BC) have been used for plotting samples chronologically.

1.1 Caves and Natural Places

In Ireland, the overwhelming quantity of human remains of Neolithic date have originated from megalithic tombs and constructed monuments, but a small and growing number of caves and natural places in the landscape have also produced Neolithic human bones. These sites have traditionally escaped attention because they lack an associated diagnostic monument and are usually only identified through radiocarbon dating. Neolithic human bones have been recovered from 16 of the 980 caves recorded across limestone regions of the country. Some of these represent formal burials accompanied by grave goods, while others indicate the secondary deposition of small quantities of human bone. More common is the evidence for excarnation rituals where corpses were laid out in caves to allow decomposition to take place naturally. Following this, larger skeletal elements were removed to another location, leaving behind small labile elements in the cave. Neolithic artefacts are not commonly found accompanying human bones in such environments, but occasionally pottery, stone axes, shell beads and animal tooth pendants have been recovered. Aside from caves, Neolithic human bones have also been occasionally discovered in bogs, lakes and rivers, often representing the secondary deposition of disarticulated bones or specific skeletal elements such as skulls.

Supplementary Fig. 1. View of Killuragh Cave (photo credit: Sam Moore).

1.1.1 Sramore Cave, Co. Leitrim

The precise location of Sramore Cave, somewhere on the northern side of Sramore Mountain near the Sligo-Leitrim border, is currently unknown[2]. Investigated by cavers in 1995, three human bones, a femur, humerus and mandible, were retrieved from the end of the main passage. Given the lack of excavation at the site, little can be said regarding the archaeological context of the remains.

The human bones most likely represent a single adult male, aged over 20 years[3]. Two radiocarbon dates have indicated this individual lived and died during the final stages of the Mesolithic. The femur returned a date of 4220-3954 cal BC (5202±36 BP, UB-6407)[4], while the mandible was dated to 4226-3963 cal BC (5227±36 BP, UB-15772)[5]. These dates fall close to the proposed establishment of agriculture on the island, raising questions as to whether the individual was associated with early farming or hunter-gatherer communities. Isotopic analysis suggests a terrestrial protein diet, showing a similar signature to Early and Late Mesolithic remains from Killuragh Cave[2]. A canine (SRA62), retrieved from the mandible, was used for DNA extraction.

Excavations at Annagh Cave were carried out in 1992[6]. The site consisted of an oval chamber entered through an opening in the cave roof, which had been blocked with a stone slab. A bipartite bowl of Linkardstown type, and a globular bowl, accompanied three inhumation burials and disarticulated remains of at least two other individuals. All individuals were identified as male or probable male, and several bore evidence of interpersonal violence. The site can be considered one of a group of burials occurring in the southern half of Ireland, closely linked in terms of burial rite, date and grave goods, generally known as 'Linkardstown cists'. Annagh Cave differs from the other Linkardstown sites listed here, however, in that it involved the appropriation of a naturally occurring geological feature, rather than the construction of a monument.

Burial 1 was a crouched inhumation of an adult male, aged 55+ years, radiocarbon dated to 3638-3137 cal BC (4670±70 BP, GrA-1703). Burial 2 was of similar age, sex and burial position to Burial 1, and radiocarbon dated to 3660-3375 cal BC (4780±60 BP, GrA-1704). Burial 3 was a male aged 30+ years at the time of death, and returned a radiocarbon date of 3705-3379 cal BC (4810±60 BP, GrA-1707). The disarticulated partial remains of at least two further individuals, labelled at publication as Burial 4 (here Burial 4/5), most likely males, returned dates of 3632-3122 cal BC (4640±60 BP, GrA-1708) and 3765-3384 cal BC (4840±60 BP, GrA-1709) respectively. An additional date for Burial 4/5 (3623-3370 cal BC, 4682±29 BP, UBA-15766) was subsequently obtained.

There is a strong possibility of kinship among these samples. Burial 1 and Burial 3 had congenitally absent third molars; and Burial 1 and Burial 4/5 (individual unclear) shared very similar expressions of complete mylohyoid bridging, a relatively uncommon trait. Burials 1, 2 and 3 had similar acetabular calcaneal facets; and the two individuals from Burial 4/5 and Burial 3 all had double anterior calcaneal facets. These shared traits could reflect responses to similar environmental stimuli,

but they could also reflect a higher than usual degree of consanguinity among these individuals[7]. The strontium isotope signatures of Burials 3 and 4/5 were seen to differ radically, however, with the 87Sr/86Sr ratio for Burial 3 (0.712042) representing the highest value of any prehistoric individual measured in Ireland to date[5]. Currently, only two individuals from Annagh Cave have been sampled for DNA extraction, Skull 1 (Burial 1) and Skull 2 (Burial 3) - ANN1 and ANN2. ANN1 consisted of the petrous portion of the individual's skull, while ANN2 was a molar sample.

1.1.3 Killuragh Cave, Co. Limerick

Killuragh Cave is one of several small caves in a limestone reef that overlooks the floodplain of the Mulkear River, a tributary of the River Shannon[8]. The cave was the subject of two archaeological excavations, in 1993 and 1996, which resulted in the recovery of disarticulated human bones, faunal remains and artefacts spanning the Early Mesolithic through to the Late Bronze Age.

Fourteen human bones from the site were radiocarbon dated, three of which were Early Mesolithic (7131-7104 cal BC, 8030±60 BP, GrA-2432; 7038-6698 cal BC, 7955±45 BP, GrA-27215; 7029-6604 cal BC, 7880±60 BP, GrA-2433) and three were Late Mesolithic (4702-4458 cal BC, 5725±55 BP, OxA-6752; 4679-4456 cal BC, 5700±40 BP, GrA-27180; 4446-4173 cal BC, 5455±50 BP, OxA-6749). A series of Early Mesolithic microliths, as well as a possible Late Mesolithic butt-trimmed flint blade, were also recovered, although these cannot be definitively associated with the human bones.

Given the absence of settlement or industrial debris, it appears that Mesolithic activities at Killuragh Cave were ritualistic in nature. There is no evidence to suggest complete bodies were interred within the system, rather, it appears that hunter-gatherers placed isolated human bones and artefacts at the mouth of the cave, which subsequently entered the system through natural processes. Its persistent use

across the Mesolithic period, coupled with its inconspicuous nature, is indicative of an important location that remained in the collective consciousness through generations[2,8].

A molar (KGH6) was selected for aDNA analysis; a direct Late Mesolithic date (4702-4458 cal BC, 5725±55 BP, OxA-6752) had been obtained from another tooth from the same context. Given the high genomic affinities of this sample to both SRA62 and continental Mesolithic samples, we assume a Late Mesolithic date for KGH6 in the current study, with a direct radiocarbon determination forthcoming.

1.14 Glennamong Boulder Chamber, Co. Mayo

The site consists of a natural boulder chamber high on the slopes of Bengorm Mountain. Rescue excavations in 2016 resulted in the recovery of disarticulated, fragmentary, unburnt human bones representing ten individuals, including elderly adult males, children and an infant. The remains were associated with a linear pit that appears to have been used for excarnation rituals, with larger skeletal elements removed from the chamber following decomposition of soft tissue, leaving behind small and fragmentary bones. A series of radiocarbon dates indicate the site was used from the Middle Neolithic through to the beginning of the Bronze Age, spanning more than a millennium[9].

Five petrous temporal bones were sampled from the site, two of which yielded endogenous contents suitable for whole genome shotgun sequencing (GNM1076 and GNM1007). These were respectively dated to 3364-2940 cal BC (4488±62 BP, UBA-37807) and 3507-3106 cal BC (4588±40 BP, UBA-38829) (Dowd in prep.).

1.1.5 Stoneyisland, Co. Galway

In 1929, turf-cutters discovered a near-complete adult skeleton beneath approximately 3m of uncut peat in a bog close to the northern shore of Lough Derg. No excavation of the site was carried out, but two descriptions of the remains were published in the 1930s[10,11]. The dating of this sample is currently

contested. Seven radiocarbon dates have been obtained from the skeleton[5,12,13]. Six dates were determined by the Oxford laboratory[12], three of which place the individual between approximately 4230 and 3800 cal BC, straddling the Mesolithic-Neolithic boundary, with a Neolithic assignment being argued by some[13,14]. Two anomalous medieval dates were also retrieved, as well as an earlier Late Mesolithic date (5323-4943 cal BC, 6200±80 BP, OxA-2758). A seventh date[5] is near identical to this latter determination (5215-5028 cal BC, 6168±31 BP, UB-15765). A portion of the right petrous temporal bone (SI118) was used for ancient DNA analysis.

1.2 Portal Tombs

Approximately 184 portal tombs are recorded in Ireland, mainly concentrated in the northern third of the country and in the south-east[15]. They conform to a standard design comprising a single rectilinear chamber, usually narrowing towards the rear, with two tall matching portal stones flanking the entrance. A capstone, often of enormous size, oversails the entrance and slopes down towards the back stone of the chamber. Closure of the entrance can range from full-height stones set between the portals to low sill-stones or, in many cases, there is no evidence of closure. A low mound surrounds the base of many of these tombs. Few examples have been excavated and only Poulnabrone (see below) has provided a comprehensive series of radiocarbon dates derived from unburnt human remains. Portal tombs and court tombs have a similar distribution and share certain structural features as well as elements of material culture. Radiocarbon dating had indicated an overlap in the period of usage of both tomb types in the mid-fourth millennium cal BC but, on present evidence, portal tombs, and Poulnabrone in particular, appear to be the earliest megalithic tombs in Ireland and belong to the early fourth millennium when farming practices were first becoming established on the island.
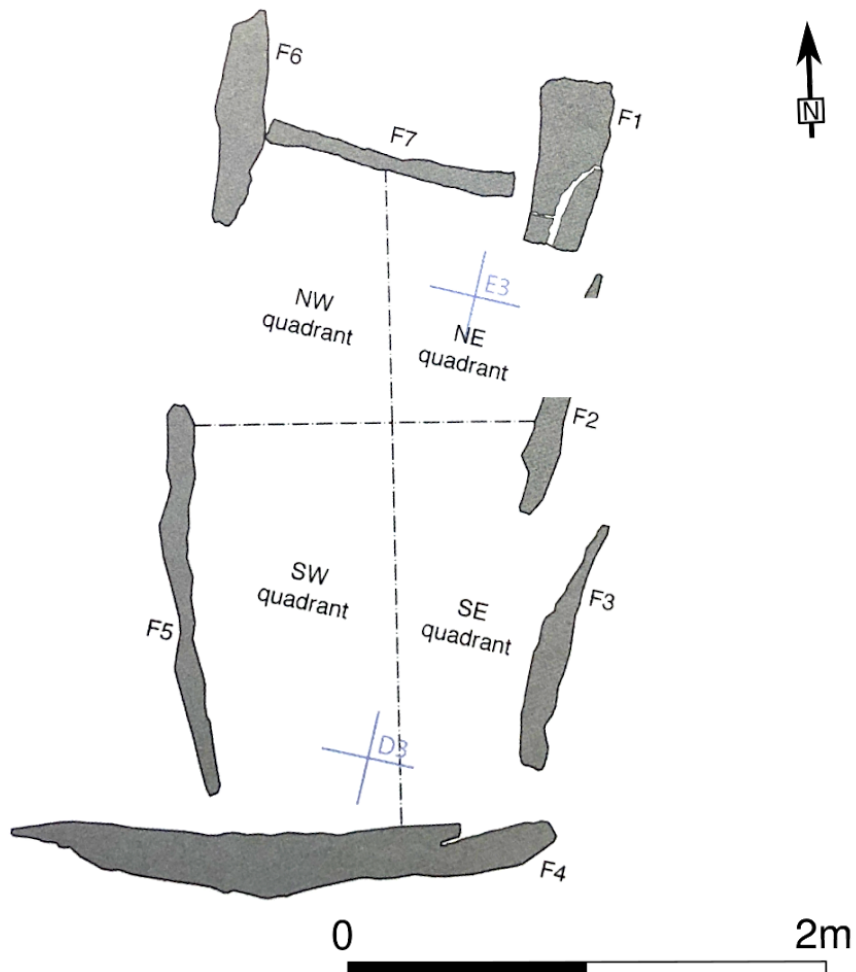
Supplementary Fig. 2. View of Poulnabrone portal tomb (Photographic Unit, National Monuments Service), with plan taken from Lynch 2014[19].

Poulnabrone portal tomb, located in a karstic region of Co. Clare known as the Burren, was excavated in the mid-1980s as part of a conservation project[16]. Excavations focused on the tomb chamber, a portico feature, and the south-west quadrant of the surrounding cairn. The unburnt, disarticulated remains of at least 35 individuals were recovered from the chamber, representing all age groups and both sexes. The predominant burial rite was successive interment with subsequent manipulation of the remains.

Poulnabrone is the most thoroughly dated portal tomb in Ireland, with a high degree of consistency between the dating programmes carried out in the late 1980s[17,18], 2010[5] and 2012 [16]. The human bones ranged in date from approximately 3800 to 3200 cal BC. The earlier dates arguably place the construction of the tomb at the very beginning of the Irish Neolithic and make Poulnabrone one of the earliest megalithic tombs in Ireland. After its construction, funerary activity continued intermittently over a period of 500-600 years. Radiocarbon dates from other portal tombs in Ireland and Britain are extremely limited, and many relate to post-Neolithic re-use.

The modelled start dates from Poulnabrone proposed by Lynch[19] (circa 3885-3710 cal BC) show no overlap with the suggested period of initial use of court tombs (3700-3550 cal BC)[20]. They also pre-date the well-defined Neolithic 'house-horizon'[21,22], the start of which has been modelled as 3720-3660 cal BC. This supports the claim of portal tombs as one of the earliest forms of Neolithic megalithic monument in Ireland[23].

Approximately 39 petrous bones were recovered from Poulnabrone, none of which had been directly dated. The majority of radiocarbon determinations for the 2012 dating programme were derived from mandibles. For this reason, three teeth from directly dated mandibles were sampled. Two of these, PN107 and PN113, were placed in the earliest phase of the Irish Neolithic (3926-3666 cal BC,

4983±30 BP, OxA-26052; 3940-3703 cal BC, 5004±31 BP, OxA-25950). The third, PN112, was chosen as an isotopic outlier and produced a slightly later date of 3696-3535 cal BC (4845±29 BP, OxA-25949).

Eleven petrous bones were also sampled, nine of which yielded endogenous contents suitable for whole genome shotgun sequencing. These were dated as part of the current study. Two petrous samples, PN04 and PN05, also returned Early Neolithic dates (3944-3665 cal BC, 4999±48 BP, UBA-38312; 3941-3661 cal BC, 4992±40 BP, UBA-38308). The dates for a further two petrous bones, PN02 and PN13, showed very close overlap with that from PN112: 3704-3522 cal BC (4834±45 BP, UBA-38313) and 3704-3536 cal BC (4854±33 BP, UBA-39199). Four of the remaining five petrous bones, PN03, PN06, PN07 and PN16, yielded extremely similar radiocarbon determinations, all close to 3635-3371 cal BC, while the date from the last petrous bone, PN12, covered a slightly wider interval (3621-3198 cal BC, 4629±41 BP, UBA-39198).
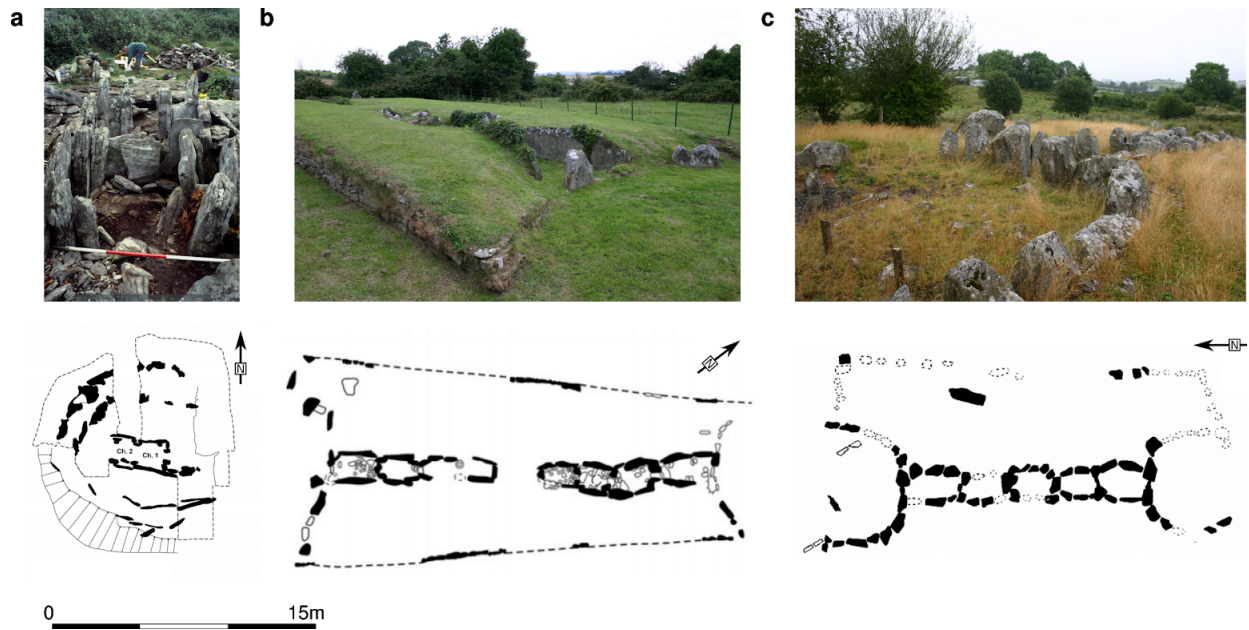
1.3 Court Tombs

There are around 400 court tombs in Ireland, concentrated in the northern half of the island. They occur most frequently in north Connacht and south Ulster but are also found more widely dispersed throughout Ulster and much of Connacht. A notable grouping of atypical southwestern court tombs (including the Parknabinnia court tomb included in this study) occurs in north Munster. Court tombs range from simple structures to much more complex forms. Simple court tombs typically consist of an elongated cairn (often trapezoidal) with a single U-shaped forecourt at the wide end leading onto a single gallery of two or more chambers arranged in sequence. The more complex court tombs are sometimes 'dual' court tombs, which have the appearance of two simple court tombs placed back-to-back, 'central' court tombs, which have the appearance of two simple court tombs placed front-to-front, and 'full-court' court tombs, where the arms of the forecourt wrap completely around the enclosing forecourt. More complex court tombs also sometimes have two galleries of chambers

placed parallel to each other and additional chambers accessed via the sides of the cairn. Most, and possibly all, of these complex court tombs are multi-phase monuments. The atypical court tombs of north Munster are distinguished by several variations in their architecture, the most notable being their small size (on average 13m long compared to more typical lengths of c. 25-35m), and their narrow straight-sided courts[24].

Bayesian modelling of radiocarbon dates from court tombs across Ireland (but primarily in the north) places the initial use of court tombs in the Early Neolithic c. 3700-3570 cal BC[20]. The initial use of court tombs appears to coincide with a distinct period of Early Neolithic activity that included the construction of large numbers of rectangular timber structures, many of which appear to have been houses, which probably occurred 50 to 150 years after the start of the Neolithic in Ireland[25,26]. While the Neolithic use of most court tombs appears to be confined to the fourth millennium BC, some (including Parknabinnia) continued to be used into the first half of the third millennium BC[20].

Architectural features of Irish court tombs reveal relationships within Ireland, as well as across the Irish Sea to the Clyde cairns of Scotland and to the Cotswold-Severn tombs of England, while the pottery, lithics and dating associated with their initial use indicate links with other Carinated Bowl-using groups. These similarities suggest connections, not only between various court tomb building groups in Ireland, but also at least historical links to groups in Britain and ultimately to northernmost France on the Continent.

Supplementary Fig. 3. Views of three court tombs sampled in the current study - **a.** Parknabinnia, **b.** Audleystown, **c.** Cohaw (Photo credits: Carleton Jones). Accompanying plans for Audleystown and Cohaw are adapted from De Valera 1960[92] (reproduced by permission of the Royal Irish Academy). The Parknabinnia plan is accredited to Carleton Jones.

1.3.1 Cohaw Court Tomb, Co. Cavan

Cohaw is a dual court tomb consisting of a rectangular cairn approximately 24 m long with a forecourt at each end. Both forecourts lead onto galleries of two chambers each and a further chamber is located at the centre of the monument which does not seem to have been accessible through either of the galleries. The site was excavated in 1949[27]. A few human teeth and some charcoal were recovered from the central chamber, while the outer chamber on the southern side of the monument (Chamber 5) contained the crushed remains of a Carinated Bowl, the partial skull of a young (probable male) individual aged between ten and fifteen years, and a small amount of cremated bone from another young individual, probably less than ten years old.

A single petrous bone (CH448) attached to a large portion of the cranium from Chamber 5 was sampled for aDNA analysis. The skull was found on the east side of the chamber resting directly on

the undisturbed subsoil that formed the floor of the chamber. It returned a date of 3652-3384 cal BC (4790±41 BP, UBA-35070).

1.3.2 Parknabinnia Court Tomb, Co. Clare

The Parknabinnia court tomb belongs to the small group of north Munster atypical court tombs. It consists of a short heel-shaped cairn approximately 10 m long, a single gallery of two chambers and a narrow, straight-sided forecourt no wider than the chambers. The site was excavated between 1998 and 2001[24]. Skeletal remains were highly fragmented but the loose limestone rubble present in the chambers provided excellent preservation conditions and over 20,000 bone fragments were recovered, 30% of which are definitely human with the majority of the remainder most likely human as well (lack of certainty due to fragmentation). At least 20 individuals were represented and these can be divided into at least 15 adults and five non-adults. The burial rite seems to have consisted of successive inhumations that were subsequently rearranged and disturbed by later inhumations[28,29]. Early Neolithic finds included Carinated Bowl pottery and leaf-shaped arrowheads. Sherds of a decorated Middle Neolithic bowl were also recovered. Prior to the current project, a series of 12 radiocarbon dates on inhumed human bone indicated that Parknabinnia was initially used c. 3700-3570 cal BC (the earliest date is 3693-3376 cal BC, 4785±60 BP, GU-10578) and then continued to be used, possibly intermittently, up into the first half of the third millennium BC (the latest date is 2905-2620 cal BC, 4195±55 BP, GU-10575)[20,24].

A total of 11 right petrous bones were sampled from both chambers of Parknabinnia, as well as its entrance, all of which were dated as part of this study. Seven individuals - PB186, PB443, PB581, PB768, PB1327, PB1794 and PB2031 - all yielded remarkably similar determinations, falling between 3647 and 3353 cal BC. Another individual, PB754, produced a similar date with a slightly wider margin of error (3617-3138 cal BC, 4622±41 BP, UBA-39196). These dates all fall within the

earlier centuries of use of Parknabinnia as defined by the wider range of dates obtained prior to the current project.

Two individuals, PB357 and PB675, were found to be approximately fourth degree relatives, however, the initial dates returned for these samples did not overlap. PB357 produced a determination very similar to the above individuals sampled (3640-3381 cal BC, 4762±37 BP, UBA-38307), while PB675 dated to 3263-2910 cal BC (4394±35 BP, UBA-35064). A brownish colour had been noted for the freeze-dried extracted collagen of PB675 in the radiocarbon facility, which potentially implies unremoved humics were present. These can make dates slightly younger and so PB675 was resubmitted for dating. The second date fell within the range obtained for PB357 and other samples (3632-3372 cal BC, 4707±42 BP, UBA-39194) and is taken as the correct one.

PB357, and another sample, PB672, were also re-dated. PB672 returned a similar but tighter distribution on re-dating (3639-3384 vs 3626-3196 cal BC; 4636±45 vs 4765±32 BP; UBA-39193 and UBA-35067). PB357 returned a slightly earlier date relative to the first determination (3774-3642 vs 3640-3381 cal BC; 4917±40 vs 4762±37 BP; UBA-39192 and UBA-38307). The average of both median probabilities are used as point estimates for the dates of these samples.

1.3.3 Audleystown Court Tomb, Co. Down

Audleystown is a dual court tomb. It consists of a 26 m long trapezoidal cairn with a shallow forecourt at each end, with both forecourts leading onto galleries of four chambers. The site was excavated in 1952 at which time both unburnt and cremated human remains, animal bones, Neolithic pottery and stone tools, and Early Bronze Age pottery were all recovered[30]. Although much of the bone assemblage was lost in a fire and flood at the Anatomy Department of Queen's University Belfast, radiocarbon dates recently obtained from some of the surviving bones produced a Late Medieval and a modern date on two cattle bones, and five Chalcolithic – Early Bronze Age dates on human bones[20].

Two undated petrous bones (AT1 and AT7) were located and sampled from the surviving assemblage. Due to their extremely low endogenous DNA contents, they were not dated as part of this study.

1.3.4 Ballyalton Court Tomb, Co. Down

The Ballyalton simple court tomb consists of an approximately 35 m long cairn with a U-shaped forecourt at its wide end that leads onto a gallery of two chambers. It was excavated in 1933 with human bone, animal bone, Neolithic pottery and stone tools all recovered[31]. The Neolithic pottery retrieved from the site led to the naming of this particular ceramic style, Ballyalton bowls[32]. Three recently obtained radiocarbon dates from the assemblage produced two Neolithic dates on human teeth and one Chalcolithic – Early Bronze Age date on cremated human bone[20].

In the current project, the two previously dated teeth, BAL329 (B76, R mandibular M2, 3649-3521 cal BC, 4796±34 BP; UB-7191) and BAL3211 (B42, L maxillary M1 3649-3385 cal BC, 4787±36 BP, UB-7192), and a single undated petrous bone, BAL14, were sampled from the assemblage.

1.3.5 Mourne Park Court Tomb, Co. Down

The Mourne Park court tomb consists of an elongated cairn, approximately 20 m long with a U-shaped forecourt at one end leading onto a gallery of two chambers. Additional orthostats in the cairn behind and adjacent to the gallery of chambers indicate the existence of further architectural complexity. The site was excavated in 1938 with both unburnt and cremated human bone, animal bone, Neolithic pottery, and much later pottery (possibly Medieval), as well as a blue glass bead recovered[33,34]. Recent sampling for radiocarbon dates produced a post-Medieval date on a sheep bone, while a human bone failed to produce a date[20]. In the current study, a single undated petrous bone (MP18) was sampled.

1.4 Passage Tombs and Affiliated

Passage tombs typically comprise a stone chamber under a round mound accessed by a passage. They are an Atlantic phenomenon, found from Iberia to Scandinavia, with significant concentrations in Ireland, Portugal, Brittany (France) and Orkney (Scotland). In Ireland there are over 220 recorded examples, dating roughly to between 3600 and 2900 cal BC, the majority of which occur within four clusters: two in County Meath, the Boyne Valley and Loughcrew, and two in County Sligo, Carrowmore and Carrowkeel. They were often placed in prominent locations dominating the surrounding landscape and some were built to massive proportions. The largest, such as Newgrange, Knowth and Dowth in the Boyne Valley, are late in the Irish series. Earlier, simpler tombs, such as those in Carrowmore, suggest these may have been a local Irish development. However, parallels with the art in earlier tombs in Brittany and on portable artefacts from Portugal suggest this did not occur in isolation.

The art includes pecked and engraved designs which appear abstract and may be derived from entoptic images observed during altered states of consciousness, but may also include symbolic or figurative representations. On earlier tombs the art was mostly restricted to the interiors thereby limiting its viewing. On some of the larger, later, tombs it adorned the external kerbstones and was meant for a wider audience. Artefacts found in Irish passage tombs include carved bone pins, stone balls and substantial carved stone basins. A particularly elaborately carved flint macehead from Knowth must have taken significant skill and time to produce. Human remains from passage tombs include cremated and unburnt bones of individuals of various ages and both sexes, but the numbers found suggest only a small portion of the communities were selected for burial within this type of tomb. The orientation of several passage tombs, such as Newgrange, suggests their builders were highly concerned with the changes of the seasons and the movement of celestial bodies, particularly the sun.
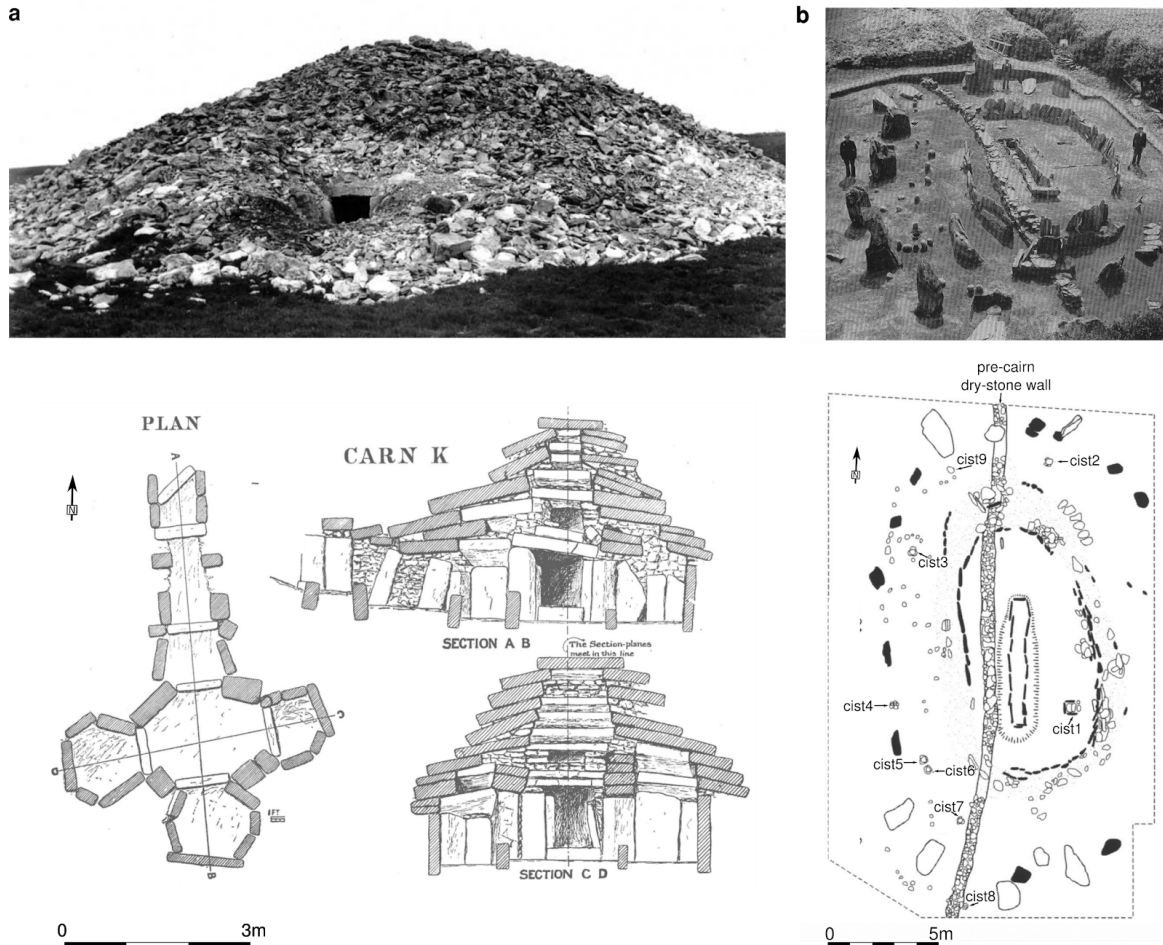
Supplementary Fig. 4. a, View, plan and elevation of Cairn K at the passage tomb cemetery of Carrowkeel taken from MacAlister *et al.* 1911[38] (reproduced by permission of the Royal Irish Academy). **b.** View and plan of the atypical Millin Bay megalithic. Photo is taken from Cooney 2000[93] (Crown copyright, HMSO), plan is after a drawing by Libby Mulqueeny in Schulting *et al.* 2012[20] (reproduced by permission of the Royal Irish Academy).

1.4.1 Newgrange Passage Tomb Complex, Co. Meath

The three great passage tombs of Newgrange, Knowth and Dowth form the core of the internationally renowned archaeological complex known as Brú na Bóinne, sited within the bend of the River Boyne and designated a UNESCO World Heritage Site in 1993. Newgrange occupies a central position within this landscape, straddling the crest of an east-west shale ridge at 56 m OD, from which the land

gently descends southwards to the floodplain of the Boyne. The remains of three smaller passage tombs also lie on the Newgrange ridge, two to the west (K and L) and one to the east (Z).

The main Newgrange tomb comprises a 19 m-long passage leading to a cruciform chamber roofed by a corbelled vault (Fig. 3). A roof-box feature above the tomb entrance allows the rays of the rising sun at the winter solstice to illuminate the passage and chamber. The tomb is covered by a flat-topped mound c. 11 m high and averaging 82 m in diameter. The base of the mound is encircled by 97 massive contiguous kerbstones, the majority greywacke, many of which are decorated with carvings. Excavations carried out in the 1960s-1970s and more recently in 1984-1988 have produced radiocarbon dates placing the construction of Newgrange in the period 3200-3000 cal BC[35,36]. Bone fragments representing a small number of people, as well as grave goods typical for Irish passage tombs, were found on the floor of the chamber during excavation[35].

The chamber had been subjected to much disturbance since it was first opened in the late seventeenth-century. However, during the excavations in 1967, human bone (burnt and unburnt), intermingled with faunal remains, was found scattered throughout the chamber area with concentrations noted in and around the left- and right-hand recesses. The unburnt bones were highly fragmented and concentrated in the area of the right-hand recess. The excavator concluded that the human remains were associated with the recesses and the radiocarbon date obtained as part of this study for sample NG10 (3338 – 3028 cal BC) places this individual at the time of the primary usage of the tomb. The unburnt material produced evidence of a minimum of two adult skeletons, one considerably larger and more heavily built. Analysis of the unburnt dental remains agree with these estimates, identifying a minimum number of two individuals, approximately 25-35 and 30-40 years in age. With the exception of one clavicle, one vertebra and the hand and foot bones, the material consisted of broken pieces. The scarcity of large limb bones, vertebral bodies and skull fragments indicate that some of the unburnt material may have been removed. Notably, neither showed any

evidence of arthritis, commonly found in Neolithic human remains. Unburnt skull fragments identified included a pair of petrous bones that closely resembled one another in their dimensions and shape. Outside the tomb, in the cairn slip and beyond, were extensive finds associated with later settlement of the Late Neolithic/Beaker periods, as well as Roman objects.

Site Z was a small passage tomb lying just to the east of the large mound. It comprised a passage of c. 9 m in length that widened gradually to form a small chamber. The diameter of the turf mound that would have covered the tomb was estimated to be c. 20 m. This tomb was systematically destroyed in antiquity whereby the structural stones of the passage, chamber and kerb were removed from their sockets and broken up. Cremated human remains were found *in situ* on the passage floor but unburnt bone, including skulls, mandibles and some long bones, had been reburied in three large pits outside the southern arc of the kerb. Based on stratigraphic evidence, the excavator suggested that Site Z post-dates the large mound of Newgrange.

A full description of human remains from site Z was made by Erskine and summarized by O'Kelly[37]. The material from the main chamber and passage of Site Z is in very fragmentary condition, however, there is mention of a right temporal bone belonging to a female, as well as two petrous portions of temporal bone, alongside other skull fragments. Skeletal material was also recovered from a 'skull pit' approximately 3 m south-west of the entrance kerbstone (K1), which stood opposite the mouth of the main passage. This consists of large fragments of three adult male skulls and one infant skull. Three temporal bones were described, two left and one right.

The majority of unburnt material from the main chamber of Newgrange was not located when sampling for this study. However, a box labelled 'cremated bone' was found and contained the aforementioned pair of unburnt petrous bones, easily identifiable given the original site report includes a photo of them[35]. The left petrous bone from the pair was sampled (NG10) and was noted to

be labeled *10 D* - corresponding to bone lot 10 from within the right-hand recess. Three temporal bones were located from Site Z, but it was unclear whether these belonged to the 'skull pits' assemblage or that from the main chamber. Two of these are left and one is right, matching the description of those recovered from the 'skull pit'. The 2 left petrous temporals were chosen for aDNA analysis (NGZ1 and NGZ2). NG10 and NGZ1 were submitted for radiocarbon dating as part of this project and produced dates overlapping with the initial period of the main chamber's construction, - yielding dates of 3338-3028 cal BC (4473±29 BP, OxA-36079) and 3320-2922 cal BC (4421±30 BP, OxA-36080) respectively.

1.4.2 Carrowkeel Passage Tomb Complex, Co. Sligo

Carrowkeel, one of the major passage tomb complexes on the island, the others being the (aforementioned) Brú na Boinne, Carrowmore, and Loughcrew complexes. It consists of a core cluster of 14 monuments spread over three limestone summits, situated within a wider megalithic landscape on and around the Bricklieve Mountains.

The main archaeological survey of the Carrowkeel tombs took place in 1911 and involved the excavation of eight passage tombs[38]. Large quantities of human remains, both cremated and unburnt, were retrieved from the tombs at that time. The assemblage was rediscovered in 2001 and has been the subject of a number of recent studies since then[39–43]. A minimum of 29 individuals were represented, including 19 adults (nine male and four female) and 10 non-adults. Evidence of dismemberment, in the form of cut marks, was found on 12 elements from two different monuments, relating to at least one individual[41].

The 40 radiocarbon dates from Carrowkeel suggest a single sequence of continuous use over most of the Neolithic period, albeit with a number of distinct changes through time. The earliest dates (prior to c. 3300 cal BC) come from cremated red deer antler fragments. These are followed by dates from

unburnt and cremated human bones, which are broadly contemporaneous with the main period of construction and use of developed Irish passage tombs[25,44], c. 3300-2900 cal BC. After c. 3000 cal BC, unburnt human skulls and skull fragments dominate the assemblage until the end of the Neolithic, with a final radiocarbon determination of 2636-2469 cal BC (at 91.5% probability, 4031±37 BP, UBA-30808) from an unburnt human skull sampled for aDNA analysis (CAK68)[42].

Eight petrous bones were sampled from the Carrowkeel assemblage. Of these, five were retrieved from Cairn K, one (most probably) from Cairn H and two from Cairn B. The two samples from Cairn B (CAK16 and CAK375) were cremated and contained no surviving human DNA. Of the remaining six samples, four yielded substantial endogenous contents and were dated for inclusion in a study by Kador et al. (42). Two of these (CAK532 and CAK533) correspond well to the main phase of activity of developed Irish passage tombs (3014-2891 cal BC, 4321±30 BP, OxA-35326 and 3085-2904 cal BC, 4360±31 BP, OxA-35327), while the others, CAK530, CAK531 and CAK68, belong to a period of Late Neolithic activity at the complex (2881-2625 cal BC, 4160±38, UBA-38306; 2883-2634 cal BC,4170±32 ,OxA-35325; 2833-2469 cal BC, 4031±37, UBA-30808).

1.4.3 Millin Bay, Co. Down

The Millin Bay multi-period site started as a dry-stone wall, adjacent to which was an elongated central cist almost 6 m in length and less than 1 m in width. The long cist was enclosed by a collection of flagstones, many of which displayed art reminiscent of that found on passage tombs, and would have been covered by an oval mound. An ovoid-shaped enclosure comprised of stone uprights was located beyond the central area of the site. Parallels have been drawn between the morphology of the Millin Bay site and the Site 3 tomb of the great passage tomb complex at Knowth, Co. Meath[45]. A large assemblage of disarticulated human bone, representing at least 15 individuals, was recovered from the interior of the long cist[46]. Cut marks relating to dismemberment were recorded on some

bones, assumed to be part of a post-mortem funerary rite, as also observed at Carrowkeel and Carrowmore[41,47]. Fragments of a single Carrowkeel bowl were found within the cairn.

Most of the Millin Bay human remains were lost until recently but were rediscovered during the current study. Prior to this rediscovery, several dates had been obtained from a small quantity of bone[20]. These dates placed the tomb usage within the second half of the fourth millennium BC, fitting with the site's developed passage tomb affinities (artwork, morphology and Carrowkeel ware pottery). However, one date was significantly earlier than expected, 3777-3652 cal BC (99.89-12b, 4937±32 BP; OxA-16598). This may indicate the deposition of ancestral relics, which pre-date the tomb's construction, or more probably, may be the result of chemical treatment with Bedacryl, a petroleum-based substance for conservation purposes which could have the effect of producing earlier radiocarbon dates[20]. Despite its clear passage tomb affinities it is notable that the tomb is located close to a number of court tombs, including that at Audleystown, also included in this study.

Prior to the rediscovery of the assemblage, two teeth recovered from dated mandibles, MB101 (3500-3133 cal BC, 4597±30 BP, OxA-16106) and MB9889 (3498-3127 cal BC, 4592±30 BP, OxA-16107), were sampled. After the rediscovery of the main collection of human remains, two undated petrous bones (MB4 and MB6) were sampled. MB6 yielded a high amount of endogenous DNA and was subsequently dated as part of the current study to within the expected range for the tomb (3495-3040 cal BC, 4548±51 BP, UBA-35071).

1.5 Unclassified

1.5.1 Ballynahatty 1855, Co. Down

The Ballynahatty 1855 (after its year of discovery) megalithic tomb was discovered immediately to the north of the well-known henge monument, the Giant's Ring. The megalith comprised a subterranean circular stone chamber, with a diameter of around 2.1 m and a height up to 1 m, radially

divided into a series of compartments. The chamber had a corbelled roof and would probably have been covered by a stone cairn. The human remains comprised a mixture of cremated and unburnt bone and it has been estimated that these represented around ten individuals. The skull of a female (A.64), with an age-at-death of 18-35 years, was recovered from Compartment D associated with disarticulated bones and fragments of cremated bone[48,49]. Radiocarbon dating of the cranium produced a result of 3342-3020 cal BC (4465±38 BP, UB-7059)[20], which places the individual in the Middle Neolithic. Based on the nineteenth-century drawings and reports, the site is considered unusual in that its morphology does not readily fit within any of the recognised megalithic tomb traditions. Decorated pottery vessels that contained cremated bone were recovered from within two compartments, and one of these was identified as Carrowkeel ware, suggesting potential passage tomb affinities.

Human bone from compartments E/F returned radiocarbon dates within the second half of the fourth millennium, the main phase of passage tomb construction. The occurrence of a variety of burial forms – cremated bone in pot, cremated bone in packages and the interment of disarticulated unburnt bone – are considered suggestive that the tomb was used for a considerable period of time, perhaps into the Early Bronze Age[49]. Two dated teeth were sampled, BA342 (right mandibular M1, 3501-3106 cal BC, 4584 ± 37 BP, UB-7521) and BA346 (left mandibular M2, 3500-3117 cal BC, 4587±34 BP, UB-7194). A left petrous from the female skull (A.64), BA64, was previously sampled and published in a separate study [50].

0   3m
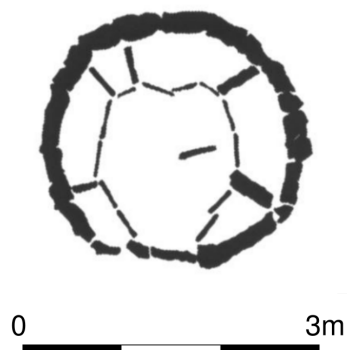
Supplementary Fig. 5. Plan of the atypical Ballynahatty 1855 megalithic, reproduced by permission of the Royal Irish Academy from Schulting et al. 2012[20] (drawn by Libby Mulqueeny).

1.6 Linkardstown-type Burials

Linkardstown cists are a small group of less than 15 monuments restricted primarily to the south-east of the country, which contrasts with the primarily northern distribution of passage tombs, court tombs and portal tombs. They are distinguished by the placement of a central stone cist within a small mound, a specific set of grave goods, a distinctive pottery style, and the presence of single, or a small number of, interments[51]. This burial form is particularly associated with adult males, though adult females and non-adults are also represented. Both articulated skeletons and quantities of disarticulated bones have been recovered from Linkardstown cists. Highly decorated bipartite bowls are a main characteristic of this burial form; other grave goods include stone axes, flint and chert implements, animal bones and shell beads. The chronology of Linkardstown burials was debated for some time, but recent dating programs centre them in the Middle Neolithic (3700-3200 cal BC)[25,51].
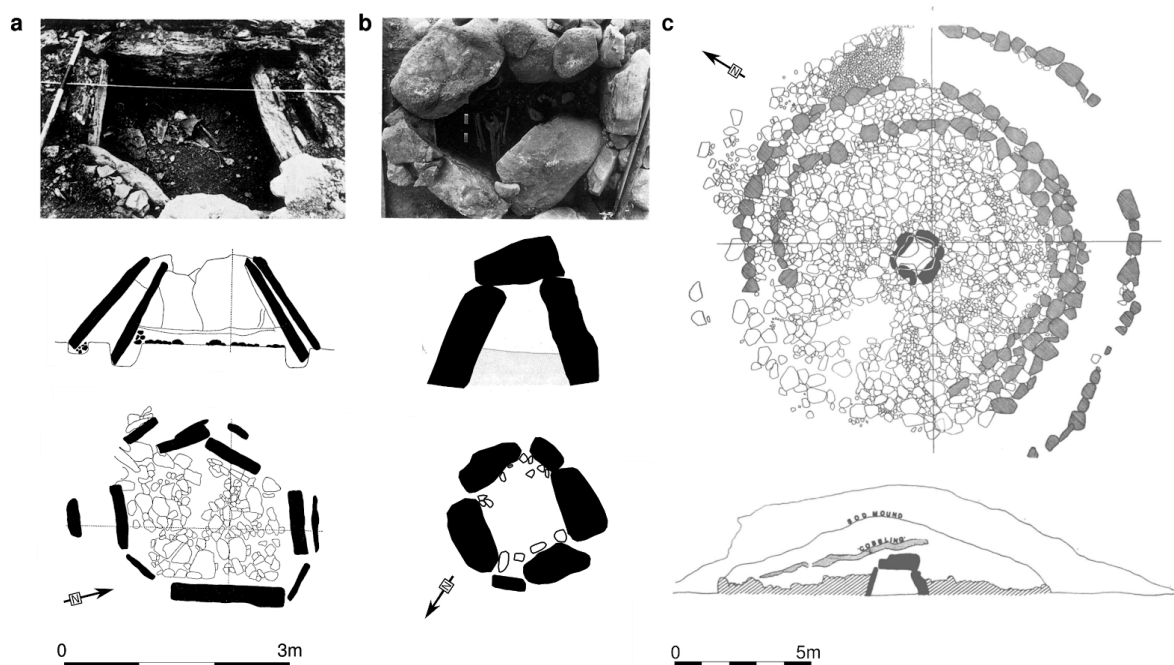
Supplementary Fig. 6. Interior views of the burial chamber with capstone removed, elevations and plans for two Linkardstown cists sampled in the current study - **a.** Jerpoint West, **b.** Baunogenasraid. Images are adapted from Ryan 1973 and Raftery 1974 respectively. **c.** Larger elevation and plan of the Baunogenasraid cairn, taken from Raftery 1974. Images are reproduced by permission of the Royal Irish Academy.

1.6.1 Baunogenasraid, Co. Carlow

The site was excavated in 1972 and 1973[52]. The primary phase consisted of a sub-megalithic structure within a low covering mound. The unburnt, disarticulated remains of an adult male were found in the northeastern corner of the chamber. The long bones were arranged together in an east-west orientation with the pelvis placed on top. The remains of the broken and incomplete skull lay nearby. A decorated, round bottom bowl was also recovered. The individual was dated to 3635-3377 cal BC (4735 ± 35 BP, GrN-11362)[51]. A petrous bone (BG72) from the Phase 1 central cist burial was sampled for aDNA analysis.

1.6.2 Jerpoint West, Co. Kilkenny

The Jerpoint West monument consisted of a polygonal cist built on the ground surface, and covered by a circular mound[53]. Grave goods included a polished bone pin, a fragment of leaf-shaped arrowhead and Neolithic ceramics. The inhumation of a young adult male (E93:15) was found within the cist, as well as the cremated remains of another individual (E93:14). The skeletal remains of a child (E93:16) of approximately six years of age were also recovered from the area.

The adult male was dated and returned two non-overlapping radiocarbon determinations one of which, GrN-11897 (3022-2878 cal BC, 4305 ± 40 BP), was discarded as anomalous when compared to the generally accepted timespan for the construction of such sites (3600 to 3300 cal BC)[45]. The other, OxA-2680 (3694-3369 cal BC, 4770 ± 80 BP), is taken to be correct[51]. An unburnt petrous bone from the inhumed adult male (E93:15) was identified for sampling. However, a labelling mistake led this sample to be associated with the registration number given to the cremated remains - E93:14. Upon arrival to the aDNA facilities the sample was given a laboratory ID of JP14 to reflect this supposed registration number. The correct registration number, E93:15, was only discovered at a late stage of analysis and thus the lab ID was not changed to reflect the archaeological ID.

1.6.3 Ardcrony, Co. Tipperary

This site consists of a cist in the centre of a denuded cairn. The disarticulated remains of two male individuals, aged as 17 and 45 years old at the time of death, lay on the floor, accompanied by a bipartite bowl[54]. The disarticulated remains of the adolescent lay along the western side of the cist, while the bones of the adult male rested on a thin layer of silt in the eastern side of the cist. A femur from the adolescent was dated[55], returning a determination of 3624-3367 cal BC (4675±35 BP, GrN-9708). Petrous temporal bones were located for the adolescent only, one of which was sampled for aDNA extraction, ARD2.

1.6.4 Ashleypark, Co. Tipperary

This site was excavated in 1980[56] and consists of a trapezoidal stone structure covered by a cairn which contained the remains of three individuals, accompanied by plain and decorated Neolithic pottery. The human bones from the chamber represented an elderly adult male and a 4-5-year-old child, both in a disarticulated and commingled state. The adult returned a date of 3641-3381 cal BC (ASH1, 4765±40 BP, GrN-11036)[51]. The bones of an infant, aged approximately eight months at the time of death, were recovered from the eastern part of the monument. Petrous bones were identified for the adult male and the infant (ASH1 and ASH3) and were sampled for aDNA analysis. ASH3 was dated as part of this study and was found to overlap chronologically with ASH1 (3712-3539 cal BC, 4876±34, UBA-38310).

1.6.5 Norrismount, Co. Wexford

The site consisted of a mound covering a central stone cist[57]. The cist contained the remains of a probable adult male, primarily skull fragments, and pottery sherds. A single disarticulated petrous (NM61) was sampled.

SI 2. Y Chromosome Analysis

Of the 37 male individuals identified, 36 had sufficient coverage for Y haplotype assessment. To determine sample haplogroups, the allelic state at each SNP in the ISOGG database (Version: 13.221, Date: 12 Sept 2018) of Y chromosomal markers was assessed. This included SNPs marked as "under investigation". The Pileup tool in GATK v2.4[58] was used to report the base calls for all reads covering each site. A minimum base quality of 30 was required for consideration. In an attempt to curtail the loss of alleles that are derived in the sample, which typically mismatch the reference genome, a relaxed mapping quality filter of 20 was maintained. Haplogroup assignments are displayed in Supplementary Tables 7 and 8.

All individuals were found to place within haplogroup I (Supplementary Table 7), with the exception of two individuals from southeastern Linkardstown burials at Jerpoint West and Baunogenasraid, JP14 and BG72, who belong to haplogroup H2 (Supplementary Table 8). Both individuals share the same subset of downstream mutations, preliminarily associated with H2a and H2a1. Haplogroup H2 is rare in both modern and ancient European populations. It has been previously observed in 12 other ancient samples from the Natufian and PPNB periods in Israel[59], the Anatolian Pottery Neolithic[60], the Spanish Neolithic and Chalcolithic[61–63], the Hungarian Early Neolithic to Beaker period[62,64,65] and Early Bronze Age Bulgaria[66].

All samples belonging to haplogroup I could be securely placed further downstream within the subclade I2a1, with the exception of the low coverage CAK534, whose placement in this clade is contingent on a single derived allele that may be the result of post-mortem damage (Supplementary Table 7). The two Mesolithic individuals, Killuragh6 (KGH6) and Sramore62 (SRA62), were found to respectively fall within the I2a1a2 and I2a1b2 subclades.

To place the Y chromosome profile of the Irish Neolithic dataset into wider geographic and temporal context, Y haplogroups were called for published ancient samples reported as haplogroup I using the same method. Male samples from all studies listed in Supplementary Table 7 were screened, as well as samples identified as haplogroup I in Olalde *et al.* 2019[63] and Scheib *et al.* 2019[67].

We present the distributions of three major subclades of haplogroup I2a1 in the European Mesolithic, Neolithic and Copper Age periods in Extended Data Fig. 7. We emphasise the lack of published samples from northwest continental Europe, an important reference point as the launchpad of agriculture into Britain and Ireland.

2.1 I2a1b

The most common haplogroup within Neolithic Ireland is I2a1b1a1a (I-M284), particularly within the portal and passage tomb sites sampled (Extended Data Fig. 7a). It has also been reported in seven individuals from an atypical court tomb in northwest Ireland[68] and is seen at high frequency in western Scotland and England[65,69]. We do not observe any incidence of this haplogroup outside the islands, however sister clades are present across Europe and display further geographic structuring (Extended Data Fig. 7b). The modern distribution of I-M284 is generally restricted to Britain and Ireland[70], suggesting some level of male lineage flowthrough on the islands from the Neolithic period.

Within the British and Irish Neolithic we observe several haplotypes associated with I2a1b1a1a1, downstream of I-M284. These are defined by the presence or absence of the derived alleles at L1193 and Y3712. Three Bronze Age samples from Britain belong to subclades even further downstream of I2a1b1a1a1, providing a temporal snapshot of the surmised flowthrough across this transition. Other I2a1b1 clades seen in ancient Europeans (Mesolithic to Bronze Age) include haplogroups I2a1b1a2a, I2a1b1a2b1~ and I2a1b1a2b3, which are all found most frequently in Eastern Europe (Extended Data

Fig. 7b), and haplogroup I2a1b1b, which appears restricted to Iberia, particularly the northeast, with the exception of one Corded Ware individual from the Czech Republic[65].

2.2 I2a1a1

Haplogroup I2a1a1b is the major lineage of the Parknabinnia court tomb. It is also observed in a single individual from the nearby Poulnabrone portal tomb and a juvenile interment within the Ashleypark Linkardstown cist (Extended Data Fig. 7a). The haplogroup is not observed in any other site in Ireland or in the British Neolithic population. We identify a suite of mutations associated with haplogroup I2a1a1b among samples from the Parknabinnia court tomb (Supplementary Table 7). Ten ancient individuals with I2a1a1b associated mutations that overlap with this "Parknabinnia haplotype" are observed in Sweden, both within the Mesolithic and Neolithic periods, as well as the Mesolithic, Neolithic and Bronze Age of Central Europe (Extended Data Fig. 7c).

2.3 I2a1a2

I2a1a2 has so far only been observed in ancient samples (Mesolithic to Bronze Age) from western Europe and Scandinavia, with highest counts and diversity seen in Iberia. Within Neolithic Britain and Ireland, the majority of I2a1a2 haplogroups occur in Orkney (Extended Data Fig. 7a). The haplogroup occurs in only five individuals from the Irish Neolithic population, four from this study and one previously reported from an atypical court tomb site[68]. Three of these individuals (CH448, PB443 and PN13) belong to haplogroup I2a1a2a1a and are ancestral for downstream mutations leading to I2a1a2a1a1 and I2a1a2a1a2. Another, ARD2 places in haplogroup I2a1a2a1a2, as do three British samples, two from Orkney. We only find incidence of I2a1a2 haplotypes with mutations overlapping with those seen in Britain and Ireland (coverage allowing) within the Iberian Peninsula (Extended Data Fig. 7d). Notably, the only Early to Middle Neolithic Orkney sample that does not fall within I2a1a2a belongs to I2a1b1a2b2, another haplogroup observed so far only within Iberia (Extended Data Fig. 7b).

29

A Late Neolithic individual from Orkney belongs to a rarer I2a1a2 haplogroup, I2a1a2a1a1. This has not yet been observed elsewhere in Britain and Ireland, but appears common in the Swedish Neolithic of Gotland Island. It is also observed in a German Neolithic individual. Another rare haplogroup, I2a1b2, is also present in Late Neolithic Orkney (Extended Data Fig. 7a). This change in the Y chromosome profile of Orkney between the Early to Middle and Late Neolithic periods may suggest an introduction of new male lineages during the transition.

Again we note potential male lineage flowthrough to the modern populations of Britain and Ireland from the Neolithic. Haplogroup I-L161 (I2a1a2a) is found today at its highest frequencies in western Ireland and the Scottish Highlands [71].

SI 3. ADMIXTURE

To estimate the different components of ancestry present in ancient Irish and Eurasian individuals in relation to diverse modern populations, we used a model-based clustering approach implemented by the program ADMIXTURE v.1.23[72]. Pseudo-haploid genotypes at ~594k known SNP positions from the Human Origins Panel[73] were called in ancient data (whole genome shotgun sequence) and those samples with over 200,000 sites called were kept for analysis. This included 138 published samples and 41 individuals from the current study (CAK534 excluded due to low coverage; PB357 and GNM1007 excluded as relatives).

Ancient calls were then merged with the modern Human Origins dataset (1,941 individuals from 198 populations) using PLINK v1.90[74]. In cases where the allele of an ancient individual matched neither of the alleles given in the Human Origins dataset, we removed this position in the ancient sample, as it is most likely the result of postmortem damage or sequencing error. In addition, 64 modern individuals from the SGDP[75], unrepresented in Human Origins, and 400 from the EGDP[76] (2 removed due to duplication in Human Origins dataset) were included to provide a larger sample of global diversity. The removal of relatives left a total of 2,387 modern individuals for analysis.

Several filters were imposed on the dataset before analysis. SNPs with a genotype missingness above 0.25 across ancient samples, and above 0.05 across the entire dataset were removed. A MAF filter of 0.05 was imposed. Finally, SNPs were pruned for sites in strong linkage disequilibrium using PLINK v1.90, with a sliding window size of 1000 variants, a step size of 50 variants, and an r^2 threshold of 0.25 (--indep-pairwise 1000 50 0.25). This left 79,122 SNPs for analysis. ADMIXTURE was run with cross-validation enabled using the --cv flag for all ancestral population numbers from K=10 to K=16. This analysis was replicated 20 times over. Median CV error was similar across all values of K,

with the lowest value seen for K=14. The results for the replicate with the highest achieved likelihood at K=14 are displayed for select ancient and modern populations in Extended Data Fig. 1a.

Eleven components reached their highest proportions in modern populations and three in ancient populations. Irish hunter-gatherers, alongside the majority of hunter-gatherers from Europe are composed entirely of a single component (red) we label *European_HG*. This is present as a minor component in the majority of European Neolithic individuals, including the Irish Neolithic. We note the individual Parknabinnia675 (PB675) has a large excess (21.45%) of the *European_HG* component, relative to the larger Irish population (median: 12.73%). If we assume successive dilutions of HG ancestry against this median value, we can place an ancestor of 100% HG ancestry for this individual within three (expected value: 23.64%) to four (expected value: 18.18%) generations ago.

The remainder of Irish Neolithic ancestry is composed almost solely of a component found at highest values in the Spanish Early Neolithic populations (orange). We label this *Early_Farmer*. We also observe some small contributions of a component highest in South Asians (green), but also present in later Iberian Neolithic and Chalcolithic populations, as well as an early Spanish Mesolithic (Chan), which is likely the result of deep structure among European HG populations[77]. Neolithic individuals from eastern and northern Europe are differentiated from those in Iberia, Ireland and Britain by the substantial contribution of two minor components - one found within in steppe, Caucasus and Iranian ancient populations (teal) and the other seen in at highest proportions in modern Bedouin individuals (cream).

SI 4. *D-* and *f*-statistics

D- and *f*-statistics[78,79] were calculated using the AdmixTools package[80] with significance assessed using a block jackknife of 5cM in size. Statistics were considered significant if they possessed a Z-score greater than 3[80], which corresponds to a p-value of less than 0.001. Pseudo-haploid calls from autosomal sites in the 1240k SNP capture[60] were used for the majority of tests involving the Irish Mesolithic population, allowing us to include available SNP capture data[60,65,66,69,81]. For outgroup f_3-statistic tests involving shotgun sequence data from the Irish Neolithic (Supplementary Information section 4.2.1), we also called pseudo-haploid genotypes for a set of ~2.7 million transversion SNPs from the 1000G Phase 3 variant panel[82], with a MAF above 0.01 in the European super-population. For both datasets, genotypes were also extracted from Mbuti individuals in the SGDP for use as an outgroup[75]. For *D*-statistics, we avoided including more than one population with data generated using the 1240k SNP capture[60] in any given test to prevent potential bias.

4.1 Genomic Affinities of the Irish Mesolithic

4.1.1 Outgroup f-statistics

We used the test f_3(Mbuti; X, IHG), where IHG represents both Sramore62 and Killuragh6 combined as a single population (see below *D*-statistics for proof they can be considered as such), to explore the affinities of Irish HGs to those on the continent (Fig. 3a). Only tests with a minimum of 10,000 informative sites were considered. Among Palaeolithic individuals, Irish HGs show closest affinity to Epigravettian individuals from Italy (Villabruna and OrienteC_HG) and an Azilian individual from Switzerland (Bichon). Among Mesolithic individuals, Irish HGs share most drift with those from the northwest of continental Europe (Loschbour, Ranchot88) and Britain (OgofYrYchen1 and CheddarMan). We took the top ten individuals of sufficient coverage with whom Irish HGs share highest drift and ran tests of the form f_3(Mbuti; HG1, HG2) for all pairs of individuals. At least 14,000 comparative sites were used in all tests. The results are plotted on a heatmap in Fig. 3a.

We tested whether Irish HGs could be considered a clade distinct from all other HG individuals in Europe through the use of the statistic D(Mbuti, X; Sramore62, Killuragh6), where X is a European Mesolithic or Palaeolithic sample (115 tests total). No significant values were obtained for any test (Supplementary Table 9). We then ran the same test with X now representing a hunter-gatherer population - British Early (BHG_EMS) and Late (BHG_LMS) Mesolithic, Caucasus (CHG), Eastern (EHG), Latvian (LVHG), Norwegian (NHG), Southeastern (Romania, Serbia and Hungary: SEHG), Spanish (SPHG) and Swedish (SWHG). We caution that the BHG_LMS population has a low total SNP coverage, which may limit our power to detect significant results. We also combined individuals from the Palaeolithic Magdalenian culture into a population (MAG), as well as Anatolian and Spanish Early Neolithics (Anatolian_EN and Spanish_EN) to test as X. Again, no significant scores were obtained.

To provide further evidence that Killuragh6 and Sramore62 can be considered as belonging to a discrete population of HGs we asked whether the two samples formed a clade distinct from Loschbour, the individual they share highest levels of drift with, as identified in outgroup f_3-statistics. The test D(Mbuti, Irish_HG1; Loschbour; Irish_HG2) was constructed and in the two possible formations significant excesses of allele-sharing were seen between the Irish HGs to the exclusion of Loschbour (Z=11.773 and Z=12.888). Given that the test D(Mbuti Loschbour; Sramore62, Killuragh6) yields an insignificant score (Z=1.358), the two Irish HGs are demonstrably distinct from northwestern continental groups. This contrasts with results from British Mesolithic genomes, which cannot be distinguished from Loschbour in this manner[69].

We applied the same principle to test whether Irish hunter-gatherers form a clade distinct from their geographically closest neighbours - British Early and Late Mesolithic populations - using the test D(Mbuti, Irish_HG1; BHG_EMS or BHG_LMS; Irish_HG2). In all four formations Irish HGs saw

significant excesses of allele-sharing with one another to the exclusion of the two British populations (Z=10.239-16.306). We also ran the test D(Mbuti, X; BHG_EMS; BHG_LMS), where X was set as Sramore62, Killuragh6 and the two combined as IHG. No significant scores were obtained. We therefore consider Irish and British HGs to belong to discrete populations.

We tested whether Loschbour, BHG_EMS or BHG_LMS share excess drift with one another to the exclusion of the Irish HG population using statistics of the form D(Mbuti X; IHG, Y). No significant score was obtained in any combination. We also tested statistics of the form D(Mbuti X; BHG_EMS or BHG_LMS, Loschbour) where X was set as Sramore62, Killuragh6 and the two combined as IHG. Again, no significant score was obtained for any test. This suggests Irish HGs are similarly distant from continental and British Mesolithic populations and supports an early split of the Irish HG lineage.

We explore the relationships between the above populations and an Epipalaeolithic individual from Grotte du Bichon, Switzerland. Despite its early date, Bichon possesses a high affinity to Irish, British and continental northwestern Mesolithic populations, as seen in outgroup f_3-statistics (Fig. 3a). Using tests of the form D(Mbuti, X; Bichon, Loschbour), we find Irish and British HGs share significant excesses of genetic drift (Z >3) with Loschbour to the exclusion of Bichon, as do a substantial number of diverse Mesolithic groups and individuals from across Europe (Supplementary Table 9).

When we change the above test to D(Mbuti, X; IHG, Bichon), only British HGs (populations and individuals) show strong evidence of breaking the clade (Z=-6.002 to -3.232), with near-significant signals from Loschbour (Z=-2.554) and another Mesolithic HG from the continental northwest, Ranchot88 (Z=-2.893). We also ran tests of the form D(Mbuti, X; BHG_EMS or BHG_LMS, Bichon). Again, significant negative values were only obtained for northwestern HGs from Britain, Ireland and the continent. We interpret our results as indicating a shared population history among

northwestern Mesolithic groups after the Epipalaeolithic period, with an earlier isolation of Irish and British HGs relative to northwestern continental groups, who show evidence of additional admixture events.

To explore the signal of additional admixtures along the lineage to Loschbour further, we ran the test D(Mbuti, X; IHG, Loschbour), where X is rotated between all populations (12 tests) and individuals (115 tests) used above (Supplementary Table 9). The majority of tests gave positive values (Z > 1), with significant results (Z >3) obtained for a number of populations and individuals, confirming that the Loschbour genome has experienced admixture from continental sources that have not impacted the Irish population. This includes significant introgression from the Magdalenian ElMiron individual (Z=4.081), as well as the wider grouping of Magdalenian samples (Z=4.13; Supplementary Table 9). Magdalenian-related ancestry is found in post-glacial western Europe during the Upper Palaeolithic and is believed to have emerged from a different glacial refugium than that from which Italian Epigravettian individuals originate[81]. Magdalenian-related ancestry was later replaced by this Epigravettian-type ancestry in western Europe, but its survival has been documented in Mesolithic Iberia[77]. Our results imply this ancestry also survived further north and contributed to lineages leading to the Loschbour individual. We also see a significant excess of allele-sharing from SPHG (Z=3.509) and the Chan_Meso individual (Z=4.309) with Loschbour, likely related to shared Magdalenian-related ancestry. Tests including Swedish HGs (Z=3.232-3.431) and the larger SWHG population (Z=2.837) also indicated shared gene flow with Loschbour to the exclusion of Irish HGs.

The above tests were repeated using the British Early Mesolithic and Later Mesolithic populations in the place of Loschbour (Supplementary Table 9). No significant scores were obtained when testing D(Mbuti, X; IHG, BHG_EMS). Only two significant scores were obtained when testing D(Mbuti, X; IHG, BHG_LMS). These indicated an excess of allele-sharing between a single Latvian HG and IHG (Z=3.082) and a single Magdalenian HG and BHG_LMS (Z=3.23), but were just over the significance

threshold and did not hold up when the larger LVHG and MAG populations were tested. To further explore, we tested D(Mbuti, X; BHG_LMS, Loschbour) and D(Mbuti, X; BHG_EMS, Loschbour). These tests produced a similar, but slightly less pronounced set of positive values as that seen for D(Mbuti, X; IHG, Loschbour). This implies that the additional admixture events detected along the Loschbour lineage occurred after its split from that leading to British and Irish Mesolithic populations, although continued interactions between Britain and the continent may have slightly reduced this signal in British HGs relative to the isolated Irish HG population. Overall, our results support the hypothesis that human occupation of Britain was extremely limited during the return to glacial conditions in the Younger Dryas, with later Mesolithic populations expanding into largely uninhabited territory[83].

4.2 Genomic Affinities of the British and Irish Neolithic

4.2.1 Outgroup f_3-statistics

We performed outgroup f_3-statistics of the form f_3(Mbuti; X, Y), across all pairs of Irish and British Neolithic individuals with whole genome sequence (whole genome capture or shotgun) available[50,68,69] (Supplementary Table 3). We did not compare British from Olalde *et al.* 2018[65] due to potential SNP capture bias. We plot the resulting distribution of f_3-statistics for all pairs with an overlap of at least 25,000 sites (1000G Phase 3 transversions with European MAF > 0.01) in Extended Data Fig. 5c. Several pairs of inflated scores were seen, corresponding to relatives identified in lcMLkin analysis.

Outgroup f_3-statistics were also used to test whether SNP-based analyses could resolve the Neolithic population structure detected using haplotype-based methods (differentiating Irish and British, Early Spanish, Later Iberian, Scandinavian and passage tomb clusters). We combined the final SNP and sample set used for the ChromoPainter[84] analysis of Atlantic genomes (Supplementary Information section 5) with genotypes from the Mbuti individuals[75]. This slightly reduced the total usable SNPs from approximately 500,000 to 400,000. Imputed genotypes were converted to homozygous to mimic

pseudo-haploid data. The results are presented as a heatmap in Extended Data Fig. 9b and show little geographic structuring.

4.2.2 D-Statistics

We explored the geographic distribution of northwestern HG (NWHG) ancestry within the British and Irish Neolithic populations (Extended Data Fig. 8a) using the test D(Mbuti, NWHG_WGS; Anatolian_Neolithic_WGS, X), where X is any Irish or British Neolithic sample (WGS or SNP capture data). NWHG_WGS represents shotgun sequence data from Loschbour, Bichon, Irish and British HGs (Supplementary Table 3). These individuals were chosen as a proxy for regional HG contribution on the basis of their shared cluster membership in FineSTRUCTURE[84] analysis (Supplementary Information section 5; Extended Data Fig. 2) and their high haplotypic donations to British and Irish Neolithic individuals (Fig. 3c). Anatolian_Neolithic_WGS represents shotgun sequence data from Anatolian Neolithic individuals (Supplementary Table 3). Only tests with over 200,000 informative sites were considered. We note an uneven geographical distribution of NWHG ancestry in the British and Irish Neolithic, with outliers observed in the west of both islands[69]. Ireland's highest values are seen in two individuals from the Parknabinnia court tomb, Parknabinnia675 and Parknabinnia754. This agrees with the results of ADMIXTURE analysis (Extended Data Fig. 1b), in which four of the five highest percentages of the *European_HG* component seen in the Irish Neolithic population are from Parknabinnia samples.

We then ran the same D-statistic test on separate chromosomes for all individuals (Extended Data Fig. 8b, c). Only tests with over 5,000 informative sites were considered. We find individuals with the highest overall levels of HG ancestry, tend to display higher variance in HG ancestry across the chromosomes, indicating more recent introgression events. The median across all individuals and chromosomes (0.05815) is close to that seen for the whole genome test in Extended Data Fig. 8a (0.0589). Larger chromosomes typically have smaller variance in levels of NWHG ancestry, with the

exception of the X chromosome which has the largest variance observed. No difference between the autosomes and X chromosome is seen in overall levels of NWHG introgression.

4.3 Genomic Affinities of car004

4.3.1 Outgroup f_3-statistics

We repeat the outgroup f_3-statistic tests from Supplementary Information section 4.2.1 using a larger SNP set of 5.6 million autosomal transversions and transitions reported in 1000G (Phase 3), with a MAF > 0.01 in at least one superpopulation of 1000G and a MAF > 0.05 in our British and Irish Neolithic population. These were called only in whole genome shotgun sequence data (whole genome capture excluded). We only considered tests with at least 25,000 usable sites. These confirm an excess amount of shared drift between car004[68] and his relatives inferred from lcMLkin (Supplementary information section 6.5) - NG10, MB6 and CAK533 (Supplementary Table 10).

4.3.2 D-Statistics

We use *D*-statistics to demonstrate that car004 forms a clade with the *passage cluster* identified within fineSTRUCTURE analysis, to the exclusion of larger British and Irish cluster, which for ease we here call the *non-passage cluster*. In this analysis, only whole genome shotgun sequence data was included. Tests were performed using two separate SNP sets, the one detailed above (Supplementary Information section 4.3.1) and the one employed in Supplementary Information section 4.2 (1000G Phase 3 transversions with European MAF > 0.01).

We ran tests of the form *D*(Mbuti, X; Y, Z), where X, Y and Z are all combinations of car004, the *passage cluster* and the *non-passage cluster* (Supplementary Table 10). Sample inclusion in these populations was based solely on fineSTRUCTURE cluster membership. Both formations that separate car004 from the *passage cluster* show significant levels of introgression between the two (Z=2.5-5.6),

while the test D(Mbuti, *non-passage cluster;* car004, *passage cluster*) yields an insignificant score (Z=0.48-0.49).

We reran the above tests several times, with the *passage cluster* replaced with NG10, MB6 and CAK533 in turn. In all cases, car004 showed significant or near-significant excesses of allele-sharing with his inferred kin, to the exclusion of the *non-passage cluster*. To test whether car004's excess affinity to the *passage cluster* is being driven by these three samples, we removed them from the *passage cluster* and reran the tests. This reduced the significance of the allele-sharing between car004 and the *passage cluster*, but a positive signal is still observed, most clearly for tests run with the larger SNP set (Z=1.5-2.3).

Given the low coverage of car004 (~0.03X WGS data), we tested the significance of our results by downsampling all BAM files for higher coverage British and Irish individuals to 0.03X. We then tested a D-statistic of the form D(Mbuti, X; *non-passage*, *passage*), where X is scrolled through the 70 downsampled British and Irish Neolithics. The *passage* and *non-passage* clusters were adjusted in each test to remove the tested individual and any relatives.

These tests were done for both SNP sets detailed above, with the larger SNP set providing approximately 116,000 usable sites per test across samples (Supplementary Table 11). The only significant results obtained (-3 > Z > 3) across all downsample tests were for CAK532 (Z=3.732) and CAK530 (Z=3.084). In contrast, Z-scores of 4.2 and 5.56 are obtained for car004 for the same test using both SNP sets. We repeated these tests for car004, removing all combinations of CAK533, MB6 and NG10 from the *passage* cluster and obtained 10 further results with Z-scores above 3.

SI 5. ChromoPainter and FineSTRUCTURE Analysis

We used ChromoPainterv2 and fineSTRUCTURE[84] to explore the haplotypic affinities of the Irish Neolithic population. We took the final dataset of 152 imputed individuals (see Methods) and removed one individual from three pairs of close relatives (GNM1007, PB357 and ans014), leaving 149 individuals for analysis.

Imputed genotypes (TVs only, GP $\geq$ 0.99, 1000G MAF $\geq$ 0.05) were filtered for a genotype missingness rate of 0 and a minor allele frequency of 0.01 or above, resulting in 363,276 autosomal sites for analysis. The genotype data was split by chromosome and phased with SHAPEIT (v2.r837)[85]. Haplotype files were converted to ChromoPainter format using "impute2chromopainter.pl" and a recombination map was created using "makeuniformrecfile.pl" both available at http://www.paintmychromosomes.com/.

After several test runs, we ran an unsupervised analysis (-a 0 0) with ChromoPainterv2 for all individuals and chromosomes using 20 E-M iterations (-i 20 -in -iM) with a starting switch rate of 250 and global mutation rate of 0.0005. We then performed principal component analysis (PCA) on the output ChromoPainter coancestry matrix of shared haplotypic lengths using the default approach available with the fineSTRUCTURE R tools package (Extended Data Fig. 2a). Irish and British Neolithic samples clustered tightly with one another, close to early Spanish Neolithic samples, with the exception of one outlier (Parknabinnia675) offsetted towards hunter-gatherer individuals.

We also ran fineSTRUCTURE's MCMC model on the same coancestry matrix for 3,000,000 million burn-in iterations and 2,000,0000 sampling iterations with no thinning. We then used the maximum concordance tree-building method described in the PoBI study[86], whereby an additional 10,000 hill-climbing moves were performed on the MCMC sample with the highest posterior probability

among all samples to reach its final inferred state. These above steps were then repeated. Both dendrograms showed identical clustering, one of which is presented in Extended Data Fig. 2b. Sample clusters correspond closely to time period with inner geographic structure present within temporal groupings.

We ran a second analysis restricted to populations of majority Early_Farmer ancestry (Supplementary section 3) from Atlantic regions. Here genotypes were filtered for a missingness rate of 0 and a more conservative minor allele frequency of 0.05 or above, leaving 488,106 autosomal sites for analysis. We also removed a single individual (PN107, CAK532, PB186 and ARD2) from four pairs of Irish samples who showed excessive haplotypic length contributions to one another (four standard deviations above the mean of their cluster; Extended Data Fig. 2b). A Swedish sample, ans017, was removed for the same reason. The starting switch and global mutation rates (245 and 0.00015) were taken from the previous run - taking the final estimated values from the "*.EMprobs.out*" output files, weighing across all chromosomes and averaging across all individuals. ChromoPainterv2 was run (-a 0 0) for all individuals and chromosomes, this time using 10 E-M iterations (-i 10 -in -iM). A PCA and 10 fineSTRUCTURE dendrograms based on the coancestry matrix of shared haplotypic lengths were constructed following the standard methods described above. The dendrograms were concordant with one another, with five major clusters identified with identical membership each time (Fig. 1d, e).

Using the coancestry matrix of haplotypic lengths from the first run above (149 individuals), we explored the relative haplotypic length contributions of HG individuals to Neolithic and Chalcolithic individuals (Fig. 3c, Extended Data Fig. 8d), as well as Early Neolithic individuals to later Neolithic and Chalcolithic individuals (Extended Data Fig. 1c). For both datasets, length donations were averaged for each donor population (defined using fineSTRUCTURE) and then normalised using the average value observed across all pairs included in the dataset. Patterns of HG donations are discussed in the main text. In the Early Neolithic analysis, we identify the Spanish Early Neolithic population as

the top haplotypic contributor to later populations from both Ireland and Iberia (Extended Data Fig. 1c). The Spanish Early Neolithic is the lowest contributor to later Neolithic and Chalcolithic populations from Greece and Central Europe, whose top contributors are earlier Greek and Central European samples respectively. The three Swedish Neolithic samples tested do not show a clear pattern, with top donations from the Iberian, LBK and Greek Early Neolithic.

Using the coancestry matrix of haplotypic lengths from the second run (Atlantic genomes), we explored the total and average haplotypic lengths shared between samples within the two clusters of Irish and British samples identified (referred to in Supplementary section 4 as the *passage cluster* and *non-passage cluster)*. To estimate average haplotypic lengths for all recipient-donor pairs we divided the total haplotypic length donated by the total number of chunks donated. Average haplotype lengths between pairs within each cluster are shown in Fig. 2d, while total haplotypic length donations are shown in Extended Data Fig. 5d.

SI 6. Estimations of Population Size, Inbreeding and Kinship

6.1 Runs of Homozygosity

Both imputed diploid genotypes and directly called diploid genotypes from higher coverage samples (>10X) were used to explore runs of homozygosity (ROH) within a dataset of 23 Mesolithic individuals. A set of 1000G biallelic transversions with a world MAF above 0.05 were used to identify ROH. We required these to be called securely in all samples (see Methods) with no missingness allowed. We included both imputed and high coverage diploid calls for the Irish hunter-gatherer SRA62. Imputed and high coverage diploid calls for three Irish Neolithic samples (NG10, PB675 and JP14) were also included for reference, as well as three modern individuals from the SGDP[75] (B_Karitiana-3, B_Mbuti-4, B_Papuan-15). After filtering for genotype missingness 606,117 SNPs were available for analysis. ROH were calculated using PLINK, with the following parameters -

--homozyg   --homozyg-density 50   --homozyg-gap 100   --homozyg-kb 500   --homozyg-snp 50 --homozyg-window-het 1 --homozyg-window-snp 50 --homozyg-window-threshold 0.05

Individual ROH were placed into two size bins over and under 1.6 Mb. Short ROH (<1.6Mb) inform on ancient population constrictions, while long ROH (>1.6Mb) reveal more recent patterns of inbreeding[87]. The fraction of the total genome under ROH was then calculated for both length categories. The masking effects of larger ROH on smaller ones were taken into account when estimating the fraction of the genome in ROH < 1.6Mb using the below calculation.

$$\frac{\text{Total Length of ROH} < 1.6 \text{ Mb}}{\text{Total genome length considered - Total Length of ROH} > 1.6 \text{ Mb}}$$

6.2 Sliding Window of Heterozygosity in Newgrange10

To visualise the larger stretches of homozygosity within the genome of NG10 we took direct diploid calls (see Methods) for all autosomal transversion SNP sites in 1000G Phase 3. After filtering this amounted to 22,982,441 million sites for analysis. We then divided his genome into 500 marker windows and calculated the percentage of heterozygote sites within each, using a 250 marker step size. The results for select chromosomes are shown in Fig. 2b. In total we identified 21 stretches of homozygosity above 20 Mb in length, several of which are larger than 40 Mb.

6.3 Inbreeding Coefficients

The results of ROH analysis indicated a high coefficient of relatedness between the parents of Newgrange10. To estimate the inbreeding coefficient (*f*) for this individual and other samples, two different measures were employed.

1. We calculated *f* using the single-point estimator implemented in PLINK (-het), which is based on the observed and expected numbers of homozygous markers. The latter value requires a large population sample from which allele frequencies can be accurately estimated. To address this need, we made use of the imputed genotypes from 46 additional Irish and British Neolithic individuals and 28 continental individuals of similar ancestry. A MAF filter of 0.05 in the sample was imposed and sites with missing genotype data excluded, leaving 432,532 sites for analysis.

2. The fraction of the genome that is within homozygous-by-descent (HBD) segments (runs of homozygosity that are identical by descent) can be used to estimate *f*. This requires the identification of ROH that are likely to be HBD, typically using a length threshold. To achieve this we followed the recommendations of Gazal *et al.* 2014[88]. Sites with missing

genotypes in our filtered imputed dataset were first removed. The dataset was then pruned for

LD (PLINK option --indep 50 2 2), which left 33,310 sites for analysis. ROH required at least

50 SNPs to be detected and no heterozygous sites were allowed. No length or density

thresholds were imposed and a sliding window of 50 SNPs was implemented (PLINK options

--homozyg --homozyg-window-het 0 --homozyg-snp 50 --homozyg-kb 1 --homozyg-density

5000 --homozyg-gap 5000). The proportion of each sample's genome in these detected

ROHs, assumed to be HBD, was then calculated using genetic length in cM.

Both methods yielded an inbreeding coefficient close to 0.25 for NG10 (0.238 and 0.245). Thus, we conclude this individual is the offspring of first degree relatives.

We plot inbreeding coefficients estimated using the HBD method for all samples in Extended Data Fig. 4 and in Fig. 1a for Irish individuals only. We note a significant decrease in inbreeding through time in ancient populations. Hunter-gatherers show both the largest variance in inbreeding coefficients and the highest median. However, none are estimated to have parents who are more closely related than four degrees. This demonstrates that the maintenance of outbreeding mating networks was common practice in the Upper Palaeolithic and Mesolithic periods of Europe, as already seen for the Sunghir site in Russia [89].

Steppe genomes from the Chalcolithic and Bronze Ages, as well as Early Neolithic genomes from Iran, Anatolia and Europe, show very similar medians and variances. We note that Iranians individuals have the highest inbreeding coefficients of the Early Neolithic sample, while Anatolian individuals from both the pottery and pre-pottery Neolithic have the lowest. This may imply different population sizes and levels of interconnectedness among farming communities in the two separate cradles of agriculture.

Successive drops in inbreeding are seen in the later Neolithic, Bronze and Iron Age populations. However, we note several outliers in the Middle Neolithic to Chalcolithic cohort. This includes the aforementioned NG10, but also an individual from a Swedish megalith (ans017), whose parents are estimated to be 3rd-2nd degree relatives. Two other individuals from the same Dolmen tomb in Ansarve, Gotland island, and another from a passage tomb in mainland Swedish, are also outliers to a lesser extent. We also note a Late Neolithic individual from the Lengyel culture in Hungary (NE7), whose parents are estimated to be fourth degree relatives.

6.4 Simulation of Inbreeding Scenarios

To explore the potential relationship between the parents of NG10, we simulated nine inbreeding scenarios that would result in an inbreeding coefficient of 0.25 (Extended Data Fig. 3b).

1. Mother-Son
2. Father-Daughter
3. Siblings
4. Double Grandfather-Granddaughter
5. Double Grandmother-Grandson
6. Double Uncle-Niece
7. Double Aunt-Nephew
8. Double Half-Siblings
9. Double Double Cousins.

Dummy genotype data was created for two founding individuals (designated "male" and "female"). 1000 offspring (500 "sons" and 500 "daughters") were then created from from this dummy data, using the sex specific recombination maps released in Bhérer *et al.* 2017[90]. A simple interference model, whereby by meioses could not occur within 10Mb of one another was adopted.

500 iterations of scenarios 1, 2 and 3, were then carried out with this data, using the same recombination maps and interference model. The 500 offspring of sibling-sibling matings, designated "grandchildren", were then mated back to both the male and female founders to model scenarios 4 and 5. These 500 *grandchildren* were also mated back to *sons* and *daughters* from whom they did not directly descend, to model scenarios 6 and 7. Finally, grandchildren were mated with one another, in combinations where they shared either one or no parents, to model scenarios 8 or 9 respectively (500 iterations each). The total numbers and average lengths of homozygous-by-descent (HBD) segments were then estimated for all iterations across all scenarios. The same values estimated for NG10 in Supplementary Information section 6.3 were then compared (Extended Data Fig. 3c).

We note that error may result in some HBD segments within the NG10 genome being split, compared to the clean dummy data. By eyeballing the whole genome heterozygosity plot for NG10 (Extended Data Fig. 3a), we identify two potential cases where this may have occurred. A small peak in heterozygosity along a ~50 Mb desert on chromosome 2, results in two HBD segments called for this region by PLINK. A peak in heterozygosity near the centromere of chromosome six, also results in two segments being identified on either side of this region. This would reduce the number of HBD segments in the NG10 genome from 35 to 33 cM and increase the average length of HBD segments from 22.99 to 24.38 cM.

6.5 Kinship Coefficients

We estimated IBD sharing between all pairs in a dataset of 86 Irish and British Neolithic samples, including 11 individuals from Sánchez-Quinto et al. 2019[68] (median coverage: 0.24X) and Brace et al. 2019[69] (median coverage: 0.018X). Only data generated through whole genome shotgun sequencing was used from these two studies, to avoid any potential bias introduced by target enrichment strategies (SNP capture or whole genome capture). Analysis was carried out using lcMLkin software,

specifically designed for low coverage sequencing data[91]. Genotype likelihoods were called for all biallelic transversion sites in the 1000G Phase 3 variant panel with a MAF above 0.01 in the European super-population using the SNPbam2vcf.py tool, recommended for lcMLkin -

(https://github.com/COMBINE-lab/maximum-likelihood-relatedness-estimation/tree/master/src_python/SNPbam2vcf).

These were subsequently filtered for a MAF above 0.05 in British and Irish Neolithic dataset. Given the high number of low coverage samples included, we chose to maximise the amount of information obtainable for each sample by creating 86 unique SNP panels, each containing all non-missing sites for a single individual. These subsets of SNPs were then extracted from the main dataset and filtered for linkage disequilibrium (vcftools --thin 25000). lcMLkin was run on all 86 datasets with the parameters set to sum over all genotypes (-g all), given their raw likelihoods (-l raw). The estimated pi-HAT scores and K_0 values were then taken for each individual from their optimised run.

This resulted in duplicate tests for all pairs of individuals in the dataset. Values calculated using less than 20,000 sites were removed (resulting in some singletons) and the remainder plotted allowing relationships to be inferred (Extended Data Fig. 5a). These were jittered slightly for visualisation purposes (pi-HAT by 0.00018 and K_0 by 0.00036). Notably, the previously reported father-daughter pair from Primrose Grange[68] (prs002 and prs017; pi-HAT: 0.455 and K_o: 0.175) were excluded from this plot, again for visualisation purposes. We also present results for car004 with a relaxed LD threshold (--thin 15000) in Fig. 2c. Given the low coverage (0.04X) of this sample, his three inferred kin connections were confirmed using outgroup f_3-statistics and D-statistics with a larger SNP set (Supplementary section 4.3).

Excluding the father-daughter pair (prs002 and prs017), we identify four pairs of relatives with a coefficient of relatedness (pi-HAT) above 0.03 (Extended Data Fig. 5a*i*) - approximately 4th degree relatives (expected pi-HAT of 0.0625) at Parknabinnia (PB675 and PB357; averaged reciprocal pi-HATs: 0.078), and approximately 5th degree relatives (expected pi-HAT of 0.03125) at Glennamong Cave (GNM1007 and GNM1076; averaged reciprocal pi-HATs: 0.033), Fussels Lodge (FusselsLodge1 and FusselsLodge2; FusselsLodge2 optimised pi-HAT: 0.033) and Primrose Grange (prs002 and prs018; prs018 optimised pi-HAT: 0.046).

This pair from Primrose Grange (prs002 and prs018), while not reported in the original study, were both documented to share a 1st and 2nd degree relationship with prs017 respectively[68]. While we detected the aforementioned 2nd degree relationship in this analysis (prs017 and prs018; reciprocal pi-HATs: 0.216 and 0.198; SNPs: 5528 and 9191), we have not plotted the result due to the number of SNP sites available for analysis being below the set threshold.

We could not confirm the 1st degree kinship between car004 and prs007 reported in the same study, given that only whole genome capture data for the latter was available to download. For the same reason, we could not test the 2nd degree kinship between prs006 and prs007. However, the 2nd degree relationship reported between car004 and prs006 was not detected in either the relaxed or stringent LD analysis for car004 (pi-HAT: 0.004-0.005, SNPs: 2085-2377) or the optimised run for prs006 (pi-HAT: 0.002, SNPs: 1427), albeit with a low number of SNP sites. We repeated, including whole genome capture data for both samples and found pi-HAT values to be only somewhat inflated (pi-HAT: 0.016-0.024, SNPs: 2091-8026).

Distant Relatives

Excluding the above pairs of close relatives (pi-HAT > 0.03), the mean pi-HAT and K_0 for the dataset were 0.0041 and 0.9919 respectively. A further 11 pairs of samples were found to have at least one duplicate outside 5 standard deviations of these values (K_0 < 0.980 and Pi-HAT > 0.0099), implying more distant kinship (5th degree or greater; pi-HAT: 0.01-0.025; Extended Data Fig. 5a*ii*).

Four of these pairs had genomic coverages of sufficient depth for inclusion in ChromoPainter[84] analysis of all ancient individuals (Extended Data Fig. 5b; see Supplementary Information section 5). Two pairs - PN04 and PN107; CAK532 and NG10 - showed an excess of haplotype sharing (outside 4 standard deviations of the mean seen between all British and Irish Neolithic samples - *passage* cluster and *non-passage* cluster), confirming their shared recent ancestry. Consequently, CAK532 and PN107 were excluded from the ChromoPainter analysis of Atlantic genomes. The two other pairs, both from Primrose Grange - prs009 and prs016; prs009 and prs013 - did not show any excesses haplotype sharing in either ChromoPainter analysis (see Supplementary section 5), despite all duplicates presenting as outliers in lcMLkin analysis.

It is unclear why this would be the case, but could due to a batch effect. We note that while all Irish data produced in this study was treated for post-mortem damage, the Primrose Grange samples were generated from several different library types[68], including both UDG and non-UDG treated double-stranded libraries, as well as single-stranded libraries, which can produce different patterns of molecular damage and thus different levels of reference bias. Samples with higher levels of reference bias may show inflated kinship estimates with one another, particularly when there is some small degree of underlying IBD-sharing already present - likely the case for the Primrose Grange population given the number of confirmed relatives already reported[68]. Imputation and haplotypic analysis should be more robust to such inflations.

Three pairs of non-UDG treated Scottish samples, published in the same study as the Primrose Grange samples[68], also show inflated kinship coefficients with one another. All pairs included the higher coverage bal004 (1.6X) from the northeast mainland and one of three lower coverage samples from Orkney. These pairings could not be tested with ChromoPainter due to low coverage. While this signal may be the result of population constrictions during the Neolithic expansion into the northeast Scotland or a distinct colonisation event, as also suggested in Y chromosome structure (Extended Data Fig. 7), it is again unclear the extent to which within lab batch effects may be having an impact.

We found one additional distant kin connection within Parknabinnia (PB672 and PB754), although again this could not be confirmed with ChromoPainter due to PB754's lower coverage.

Finally, three pairs included the early passage tomb sample, car004[68], and later passage tomb samples from Carrowkeel, Newgrange and Millin Bay. The latter test fell just below the threshold of sites imposed (19,850; transparent point on Extended Data Fig. 5a*ii*). Given the importance of this low coverage passage tomb sample, we repeated lcMLkin analysis with a relaxed LD filter (--thin 15000; Fig. 2c) and found the same results. *D*- and outgroup f_3-statistics further confirm this excess of allele-sharing between car004 and other passage tomb samples, which is discussed in Supplementary section 4.2. We also downsampled the BAM files of all higher coverage individuals to the same coverage as car004 (~0.03X) and repeated the optimised lcMLkin analysis on each. No inflated kinship coefficients ($K_0 < 0.980$ and Pi-HAT > 0.0099) were obtained for any sample pair that had not already been identified in the initial analysis, with the exception of CAK533 and MB6 (K_0: 0.980 and Pi-HAT: 0.011), who are noted to share elongated haplotypes with one another in Fig. 2d.

Other pairs with excess haplotype-sharing

We note that two other sample pairs (ARD2 and PB443; PB186 and PN06) showed a significant excess of haplotypic sharing in ChromoPainter analysis (Extended Data Fig. 5b), but had pi-HAT

values lower than 0.01 in lcMLkin analysis. However, both ARD2 and PB443 were reciprocal top hits for one another (pi-HATs: 0.008 and 0.0085). PB186 was the top hit for PN06's optimised run (pi-HAT: 0.0075), while PN06 was the second highest hit for PB186's run (pi-HAT: 0.006) after PN07 (pi-HAT: 0.007). Interestingly, PN07's top haplotype donor and recipient is PB186, while PB186's second highest haplotypic donor and recipient is PN07, after PN06. This implies distant familial links between the neighbouring tombs of Parknabinnia (PB186) and Poulnabrone (PN06 and PN07).

Final note on kinship within the two Burren sites

We observe that despite the large samples taken from both Parknabinnia (n=11) and Poulnabrone (n=13), only several kin pairings were found. Indeed, while no close relatives were found at Poulnabrone, we identified two samples - a tooth (PN113) and a petrous (PN10) - as belonging to the same individual in a screening run of lcMLkin. Double sampling from disarticulated remains suggests a sizable portion of the surviving interments have been sampled. These results imply the sites were not used solely by close kin groups. Notably, the only kin connection (PN04 and PN107) seen at Poulnabrone comes from the earliest phase of the site's usage, falling at the very beginning of the Irish Neolithic. However, these two individuals are only distantly related and show no relationship to other individuals dated to the same phase. Excluding the possibility that these remains were ancestral relics brought to Ireland from Britain or the continent, these findings, together with estimated inbreeding coefficients, suggest a large community was availing of the site from the very outset of its construction.

References

1. Reimer, P. J. *et al.* IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon* **55**, 1869–1887 (2013).

2. Dowd, M. *The Archaeology of Caves in Ireland*. (Oxbow Books, 2015).

3. Fibiger, L. Osteoarchaeological analysis of human skeletal remains from 23 Irish caves. in *Underground Archaeology. Studies on Human Bones and Artefacts from Ireland's Caves* (ed. Dowd, M.) 3–37 (Oxbow Books, 2016).

4. Dowd, M. A. The use of caves for funerary and ritual practices in Neolithic Ireland. *Antiquity* **82**, 305–317 (2008).

5. Kador, T., Fibiger, L., Cooney, G. & Fullagar, P. Movement and diet in early Irish prehistory: First evidence from multi-isotope analysis. *J. Ir. Archaeol.* **23**, 83–96 (2015).

6. Ó Floinn, R. Annagh, Co. Limerick, 92E047. in *Breaking Ground, Finding Graves: Reports on the Excavations of Burials by the National Museum of Ireland, 1927-2006, volume 1* (eds. Cahill, M. & Sikora, M.) 17–33 (Wordwell Ltd., 2011).

7. Ó Donnabháin, B. Annagh Cave. Human remains. in *Breaking Ground, Finding Graves–Reports on the Excavations of Burials by the National Museum of Ireland, 1927-2006, volume 1* (eds. Cahill, M. & Sikora, M.) 34–47 (Wordwell Ltd., 2011).

8. Woodman, P., Dowd, M., Fibiger, L., Carden, R. F. & O'Shaughnessy, J. Archaeological excavations at Killuragh Cave, Co. Limerick: a persistent place in the landscape from the Early Mesolithic to the Late Bronze Age. *J. Ir. Archaeol.* **26**, 1–32 (2017).

9. Dowd, M. & Lynch, L. *Final excavation report. Rescue excavation of Neolithic human remains from a natural boulder chamber in Glennamong townland, Bengorm Mountain, Co. Mayo. SMR: MA057-005. Licence number: 16E0456. Unpublished report submitted to the National Monuments Service and the National Museum of Ireland*. (2017).

10. Shea, S. Report on the human skeleton found in Stoney Island Bog, Portumna. *Galway Archaeol. Histor. Soc. iety* **15**, 73–79 (1931).

11. Martin, C. P. *Prehistoric Man in Ireland*. (Macmillan, 1935).

12. Hedges, R. E. M., Housley, R. A., Bronk, R. C. & van Klinken, G. J. Radiocarbon dates from the Oxford AMS system: Archaeometry Datelist 17. *Archaeometry* **35**, 305–326 (1993).

13. Brindley, A. L. & Lanting, J. N. Irish bog bodies: the radiocarbon dates. *Bog Bodies: New discoveries and New Perspectives* 133–136 (1995).

14. Woodman, P. Getting back to basics: transitions to farming in Ireland and Britain. *Europe's First Farmers* (ed. Douglas Price, T.) 219–259 (Cambridge University Press, 2000).

15. Kytmannow, T. Portal tombs in the landscape: the chronology, morphology and landscape setting of the portal tombs of Ireland, Wales and Cornwall. (British Archaeological Reports Oxford Ltd 2008).

16. Lynch, A. *Poulnabrone: An Early Neolithic Portal Tomb in Ireland*. (Stationary Office, 2014).

16. Lynch, A. *Poulnabrone: An Early Neolithic Portal Tomb in Ireland*. (Stationary Office, 2014).

17. Hedges, R. E. M., Housley, R. A., Law, I. A. & Bronk, C. R. Radiocarbon dates from the Oxford AMS system: Archaeometry Datelist 10. *Archaeometry* **32**, 101–108 (1990).

18. Lynch, A. & Donnabháin, B. O. Poulnabrone portal tomb. *The Other Clare* **18**, 5–7 (1994).

19. Schulting, R. J. The dating of Poulnabrone, Co. Clare. in *Poulnabrone: An Early Neolithic Portal Tomb in Ireland* (ed. Lynch, A.) 93–113 (Stationery Office, 2014).

20. Schulting, R. J., Murphy, E., Carleton Jones & Warren, G. New dates from the north and a proposed chronology for Irish court tombs. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **112C**, 1–60 (2012).

21. McSparron, C. 'Have you no homes to go to?' *Archaeol. Ir.* **22**, 18–22 (2008).

22. Cooney, G. In Retrospect: Neolithic activity at Knockadoon, Lough Gur, Co. Limerick, 50 years on. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **107C**, 215–225 (2007).

23. Whittle, A. Stones that float to the sky: portal dolmens and their landscapes of memory and myth. in *The Neolithic of the Irish Sea: Materiality and Traditions of Practice* (eds. Cummings,

V. & Fowler, C.) 81–90 (Oxbow Books, 2004).

24. Jones, C. The north Munster atypical court tombs of western Ireland – social dynamics, regional trajectories and responses to distant events over the course of the Neolithic. in *Megaliths - Societies - Landscapes. Early Monumentality and Social Differentiation in Neolithic Europe* (eds. Müller, J., Hinz, M. & Wunderlich, M.) 979–1000 (Habelt Verlag, 2019).

25. Cooney, G. *et al.* Chapter 12: Ireland. in *Gathering Time: Dating the Early Neolithic Enclosures of Southern Britain and Ireland* (eds. Whittle, A., Healy, F. & Bayliss, A.) 562–669 (Oxbow Books, 2011).

26. Smyth, J. *Settlement in the Irish Neolithic: New Discoveries at the Edge of Europe*. (Oxbow Books, 2014).

27. Kilbride-Jones, H. E. & Keenan, E. Double Horned Cairn at Cohaw, County Cavan. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **54**, 75–88 (1951).

28. Beckett, J. Selective burial in Irish megalithic tombs: burial practice, age, sex and representation in the Neolithic. in *Proceedings of the Fifth Annual Conference of the British Association for Biological Anthropology and Osteoarchaeology* 31–39 (2005).

29. Beckett, J. & Robb, J. Neolithic burial taphonomy, ritual, and interpretation in Britain and Ireland: a review (eds. Gowland, R. & Knüsel, C.) *Social Archaeology of Funerary Remains* 57–80 (2006).

30. Collins, A., Morton, W. & Scott, J. H. The excavation of a double horned cairn at Audleystown, Co. Down. *Ulster J. Archaeol.* 7–56 (1954).

31. Evans, E. E. & Davies, O. 111. Excavation of a Horned Cairn at Ballyalton, Co. Down. *Man* **34**, 88–90 (1934).

32. Case, H. Irish Neolithic pottery: distribution and sequence. *Proc. Prehist. Soc.* **27**, 174–233 (1961).

33. Davies, O. Excavations at Mourne Park. *Proc. Belfast Nat. Hist. Phil. Soc.* **1**, 18–26 (1938).

34. Herity, M. The Finds from Irish Court Tombs. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist.*

Linguist. Lit. **87C**, 103–281 (1987).

35. O'Kelly, M. J. *Newgrange*. (Thames and Hudson, 1983).

36. Lynch, A. Newgrange revisited: new insights from excavations at the back of the mound in 1984–8. *J. Ir. Archaeol.* (2014).

37. O'Kelly, M. J. *et al.* Three Passage-Graves at Newgrange, Co. Meath. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **78**, 249–352 (1978).

38. Macalister, R. A. S., Armstrong, E. C. R. & Praeger, R. L. Report on the Exploration of Bronze-Age Carns on Carrowkeel Mountain, Co. Sligo. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **29**, 311–347 (1911).

39. Robert Hensey, Pádraig Meehan, Marion Dowd & Sam Moore. A century of archaeology—historical excavation and modern research at the Carrowkeel passage tombs, County Sligo. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **114C**, 57–87 (2014).

40. Geber, J., Hensey, R., Meehan, P., Moore, S. & Kador, T. Reassessing the Age, Sex and Metric Variation of Commingled Human Remains from a 1911 Excavation of a Neolithic Passage Tomb Complex in North-West Ireland. *Int. J. Osteoarchaeol.* **27**, 131–142 (2017).

41. Geber, J. *et al.* Facilitating Transitions: Postmortem Processing of the Dead at the Carrowkeel Passage Tomb Complex, Ireland (3500–3000 cal. B.C.). *Bioarchaeol. Int.* **1**, 35–51 (2017).

42. Kador, T. *et al.* Rites of Passage: Mortuary Practice, Population Dynamics, and Chronology at the Carrowkeel Passage Tomb Complex, Co. Sligo, Ireland. *Proc. Prehist. Soc.* **84**, 225–255 (2018).

43. Meehan, P. & Hensey, R. Carrowkeel to Cambridge: resolving the origins of a Neolithic bone assemblage. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **118C**, 1–36 (2018).

44. O'Sullivan, M. *Duma na nGiall: Tara The Mound of the Hostages*. (Wordwell Ltd., 2005).

45. Waddell, J. *The Prehistoric Archaeology of Ireland*. (Galway University Press, 1998).

46. Collins, A. E. P., Waterman, D. M., Morton, W. & Scott, J. H. *Millin Bay: A Late Neolithic Cairn in Co. Down: With an Account of the Human Skeletal Material*. (HM Stationery Office,

1955).

47. Murphy, E. Funerary processing of the dead in prehistoric Ireland. *Archaeol. Ir.* **17**, 13–15 (2003).

48. MacAdam, R. & Getty, E. Discovery of an ancient sepulchral chamber. *Ulster J. Archaeol. ogy* **3**, 358–365 (1855).

49. Hartwell, B. The prehistory of the Giant's Ring and Ballynahatty townland. *Lisburn Hist. Soc. J.* **9**, (1995).

50. Cassidy, L. M. *et al.* Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 368–373 (2016).

51. Brindley, A. L. & Lanting, J. N. Radiocarbon Dates for Neolithic Single Burials. *J. Ir. Archaeol.* **5**, 1–7 (1989).

52. Raftery, B. A Prehistoric Burial Mound at Baunogenasraid, Co. Carlow. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **74**, 277–312 (1974).

53. Ryan, M. F. The Excavation of a Neolithic Burial Mound at Jerpoint West, Co. Kilkenny. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **73**, 107–127 (1973).

54. Wallace, P. F. A prehistoric burial cairn at Ardcrony, Nenagh, Co. Tipperary. *North Munster Antiquarian J.* **19**, 3–20 (1977).

55. Brindley, A. L., Lanting, J. N. & Mook, W. G. Radiocarbon Dates from the Neolithic Burials at Ballintruer More, Co. Wicklow and Ardcrony, Co. Tipperary. **1**, 1–9 (1983).

56. Manning, C. *et al.* A Neolithic Burial Mound at Ashleypark, Co. Tipperary. *Proc. R. Ir. Acad. C Archaeol. Celt. Stud. Hist. Linguist. Lit.* **85C**, 61–100 (1985).

57. Lucas, A. T. Neolithic Burial at Norrismount, Co. Wexford. *J. R. Soc. Antiq. Irel.* **80**, 155–157 (1950).

58. McKenna, A. *et al.* The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res.* **20**, 1297–1303 (2010).

59. Lazaridis, I. *et al.* Genomic insights into the origin of farming in the ancient Near East. *Nature*

536, 419–424 (2016).

60. Mathieson, I. *et al.* Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499–503 (2015).

61. Günther, T. *et al.* Ancient genomes link early farmers from Atapuerca in Spain to modern-day Basques. *Proc. Natl. Acad. Sci. U. S. A* **38,** 11917-11922 (2015).

62. Haak, W. *et al.* Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207–211 (2015).

63. Olalde, I. *et al.* The genomic history of the Iberian Peninsula over the past 8000 years. *Science* **363**, 1230–1234 (2019).

64. Lipson, M. *et al.* Parallel palaeogenomic transects reveal complex genetic history of early European farmers. *Nature* **551**, 368–372 (2017).

65. Olalde, I. *et al.* The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature* **555**, 190–196 (2018).

66. Mathieson, I. *et al.* The genomic history of southeastern Europe. *Nature* **555**, 197–203 (2018).

67. Scheib, C. L. *et al.* East Anglian early Neolithic monument burial linked to contemporary Megaliths. *Ann. Hum. Biol.* **46**, 145–149 (2019).

68. Sánchez-Quinto, F. *et al.* Megalithic tombs in western and northern Neolithic Europe were linked to a kindred society. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 9469–9474 (2019).

69. Brace, S. *et al.* Ancient genomes indicate population replacement in Early Neolithic Britain. *Nat. Ecol. Evol.* **3**, 765–771 (2019).

70. International Society of Genetic Genealogy. Y-DNA Haplogroup I and its Subclades. *isogg.org* (2017). Available at: https://isogg.org/tree/ISOGG_HapgrpI.html.

71. Gabel, R. I-L161 (I2a-Isles). *https://www.familytreedna.com* (2019). Available at: https://www.familytreedna.com/groups/i-2a-l161/. (Accessed: 2019)

72. Alexander, D. H., Novembre, J. & Lange, K. Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* **19**, 1655–1664 (2009).

73. Lazaridis, I. *et al.* Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* **513**, 409–413 (2014).

74. Chang, C. C. *et al.* Second-generation PLINK: rising to the challenge of larger and richer datasets. *Gigascience* **4**, 7 (2015).

75. Mallick, S. *et al.* The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature* **538**, 201–206 (2016).

76. Pagani, L. *et al.* Genomic analyses inform on migration events during the peopling of Eurasia. *Nature* (2016). doi:10.1038/nature19792

77. Villalba-Mouco, V. *et al.* Survival of Late Pleistocene Hunter-Gatherer Ancestry in the Iberian Peninsula. *Curr. Biol.* **29**, 1169–1177.e7 (2019).

78. Green, R. E. *et al.* A draft sequence of the Neandertal genome. *Science* **328**, 710–722 (2010).

79. Reich, D., Thangaraj, K., Patterson, N., Price, A. L. & Singh, L. Reconstructing Indian population history. *Nature* **461**, 489–494 (2009).

80. Patterson, N. *et al.* Ancient admixture in human history. *Genetics* **192**, 1065–1093 (2012).

81. Fu, Q. *et al.* The genetic history of Ice Age Europe. *Nature* **534**, 200–205 (2016).

82. McVean, G. A. *et al.* An integrated map of genetic variation from 1,092 human genomes. *Nature* **491**, 56–65 (2012).

83. Pettitt, P. & White, M. *The British Palaeolithic: Human Societies at the Edge of the Pleistocene World*. (Routledge, 2012).

84. Lawson, D. J., Hellenthal, G., Myers, S. & Falush, D. Inference of population structure using dense haplotype data. *PLoS Genet.* **8**, e1002453 (2012).

85. Delaneau, O., Marchini, J. & Zagury, J.-F. A linear complexity phasing method for thousands of genomes. *Nat. Methods* **9**, 179–181 (2011).

86. Leslie, S. *et al.* The fine-scale genetic structure of the British population. *Nature* **519**, 309–314 (2015).

87. Pemberton, T. J. *et al.* Genomic Patterns of Homozygosity in Worldwide Human Populations.

Am. J. Hum. Genet. **91**, 275–292 (2012).

88. Gazal, S. *et al.* Inbreeding coefficient estimation with dense SNP data: comparison of strategies and application to HapMap III. *Hum. Hered.* **77**, 49–62 (2014).

89. Sikora, M. *et al.* Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers. *Science* **358**, 659–662 (2017).

90. Bhérer, C. *et al.* Refined genetic maps reveal sexual dimorphism in human meiotic recombination at multiple scales. *Nat. Commun.* **8,** 14994 (2017) .

91. Lipatov, M., Sanjeev, K., Patro, R. & Veeramah, K. Maximum Likelihood Estimation of Biological Relatedness from Low Coverage Sequencing Data. *bioRxiv* 023374 (2015). doi:10.1101/023374

92. De Valera, R. The court cairns of Ireland. *Proceedings of the Royal Irish Academy: Archaeology, Culture, History, Literature* **60C**, 9–140 (1960).

93. Cooney, G. *Landscapes of Neolithic Ireland.* (Routledge, 2012).